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A MATHEMATICAL REPRESENTATION
OF THE RESPONSE OF THE PLANT TO TIME

ir. W. C. Visser

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A MATHEMATICAL REPRESENTATION OF THE RESPONSE OF THE PLANT TO TIME

ir. W. C. Visser

Mathematical treatment of complex biological problems

Soil fertility is a problem that is particularly suited for solution by computer models. In such a model the influences of beneficial as well as adverse growth factors can be described in a comprehensive way.

Much is known about the reaction of crops on the growth factors separately. This we will call the special aspects of the processes. Soil productivity, however, is dependent on the effect of all factors combined.

This integrated problem necessitating that the special processes are inserted in a general reaction pattern, is not unduly complicated because all factors are taken up by the process of diffusion. Some other transport processes may also have an influence, such as mass-flow, but these mechanisms of nutrient uptake and the counteraction of adverse influences have in common that they can be represented by linear transport equations.

The number of growth factors is large and therefore the effect of many of them taken separately must be small. General interest has mainly been directed towards the 15 to 20 beneficial factors. Because the farmer has gradually corrected deficiencies in these beneficial factors, the importance of the adverse factors, of which there are several hundreds, require in an ever increasing way that careful investigations should be carried out.

Up to now the adverse factors have received far less attention than the beneficial ones. Possibly the often studied salinity factor is an exception.

Also the influence of time has obtained some, however restricted, interest. This has led to the development of exponential and

logistic functions (PATTON, 1971). But a mathematically treated plant physiological basis does not seem to have been studied in sufficient detail.

It is interesting to compare the scientific approach of soil fertility studies - as was mentioned already, largely a problem of diffusion and mass flow or root expansion as processes for the transport of fertilizers in aqueous solution - with the scientific concept which provides the basis of the studies on groundwater flow.

In the latter study, the interest has of late been switched from the elaboration of separate processes of groundwater flow - such as drainage, capillary rise or evaporation - to the integrated study of combined processes of water flow and water storage. This is becoming a study of the dynamic water balance, which has much in common with the dynamic fertilizer balance.

This type of hydrologic research, aiming at the integrated representation of the entire problem, is more advanced in hydrology than in soil fertility research. This hydrologic research might be used as an example and a guide in other fields of comprehensive study especially in fertility research. Such an integrated research can be complementary to the specialized studies of single factors. Other growth factors are discussed elsewhere (VISSER, 1968; 1969).

The hydrologic research here referred to is part of an investigation into the effect of water abstraction for civil water supply on the productivity of agricultural land in an area with a groundwater table shallow enough to enable capillary contact between the plant roots and the groundwater table. The practical results will be of prime importance, but require the use of the best scientific theory available. Only a theory with respect to the effect of time on plant growth will be discussed in this article, considerations based on practical application will be mentioned if necessary.

Special processes and basic response patterns

The reaction pattern of the response of a plant on a growth factor has to fit into the general pattern, accounting for the basic process of nutrient uptake.

An instance for this general pattern is the equation accounting for a simple diffusion process, as represented by

$$\left(1 - \frac{q}{a(x-x_0)}\right) \left(1 - \frac{q}{b(y-y_0)}\right) \dots = F \quad (1a)$$

and

$$\left(1 - \frac{\Delta q}{a(\Delta x - \Delta x_0)}\right) \left(1 - \frac{\Delta q}{b(\Delta y - \Delta y_0)}\right) \dots = F \quad (1b)$$

where x and y represent growth factors with activity constants a and b (VISSER, 1968). The yield is represented by q . F is mathematically an integration constant. The biological significance is that of an elasticity. That is the variability in the quantitative value of the ratio, according to which the plant is able to build its matter with slightly varying proportions of the different growth factors.

Superimposed on the basic response pattern are the special processes of plant response.

In formula (1) this special process is represented by

$$\begin{aligned} q' &= a(x - x_0) \\ q'' &= b(y - y_0) \end{aligned} \quad (2)$$

These equations describe the reactions of a plant on a single growth factor.

Equation (1) and (2) lead to a plant growth equation:

$$\left(1 - \frac{q}{q'}\right) \left(1 - \frac{q}{q''}\right) \dots = F$$

Here q is the yield for all the growth factors combined, while q' and q'' represent the yields for the single effect of the factors x and y .

In the following discussion time has to be defined as a special factor, which definition, as generally is the case with the factor time, will represent a rather complicated reaction pattern.

In hydrology the more complicated patterns are generally the result of a non-steady stream flow. In plant physiology the time-dependent effects are not necessarily dependent on non-steady relations. The storage capacity of the plant is too small for a number

of factors to make non-steady situations inside the plant of sufficient importance to devote a study to them.

The special processes, as described in formula 2 may be expected to be of a linear type. If q is linked with x or y by a more complicated equation, this will point to the fact that q was not linked to the factor x from which the plant response originates. The process apparently is described for an intercalated factor u which makes the relation non-linear:

$$\begin{aligned}x &= f(u) \\q' &= a \left(f(u) - f(u_0) \right) \quad (3)\end{aligned}$$

In these linear reaction patterns, describing the effect of time, important singular points as germination or the death of the plant should be represented mathematically, as they occur in reality. These singular moments in plant development coincide with the beginning and end of plant life and should necessarily be represented in an acceptable definition of plant response.

Mutually independent basic plant response patterns

In a complete integrated model for plant response an indicated place in the mathematical model should be reserved for all main reaction patterns as dry matter production, growth rhythm, diversity of species in plant associations, quality of the yield and probably some other main aspects of plant reaction as for instance plant health.

Generally it may be assumed that if the problem of plant response is observed from a plant physiological angle, aspects as dry matter production and the diversity of species in a plant association will be considered as mutually independent. It are entirely different reactions of the plant, governed by different factors.

Mathematically such an independence is shown by the shape of the formula which in such a case would read:

$$f(q) dq = f(t) dt$$

Lack of independence complicates the equation of response and may make an exact integration impossible. In case of a mutual dependence

the formula might be:

$$f(q, t) dq = dt$$

Such a formula often will not allow to split the function up in integrable q- and t-parts.

The independence is shown by an additive mutual relation, which does not possess interactions.

The habitual concept of independency does not accept an influence on both q and t by a common third factor as different from an interaction. An interaction, however, would nullify the independence, the third factor would not.

The relation between the mutually independent response patterns is of importance to give the model a correct shape. For dry matter production and growth rhythm the model is built up on

$$dC = c dT \quad (4)$$

Here dC defines the change in the rate of cell division C. In dT one recognizes the increase in the plant physiological time T, well to be distinguished from the real time t.

The plant physiological time represents a time influence identical to the cause of the plant response. A lower temperature slackens the progress of the time as it is experienced by the plant. This plant physiological time T agrees with the change in the rate of cell division according the linear relation of formula (4).

It will be clear that independence is given here meaning differing from the mathematical as well as the plant physiological one. Independence is considered to exist if the change in one factor does not modify the shape of the curve for the relation with another factor and only influences the level of the curve. This definition of independence, however, is of importance for it assists in selecting the correct model in case the different types of plant response are considered to be mutually dependent or independent.

Basic properties of the time-yield function

The T-function is the predetermined place for the effects of many kinds of human intervention, as the advancement of plant growth,

the ripening of fruits, the blooming of flowers, the jarowisation of seeds, the growing of a vegetable species around the year. This amounts to the description of life and death, juvenility and senescence of the plant.

This T-function is directly independent of the dry matter production, though the relation with the time effect may be indirect because for instance both dry matter production and growth rhythm are dependent on temperature.

The shape of the curve for the time effect is based on the experience with the logistic time - yield curve. It is assumed that the rate of cell division dC/dq reacts according to the number of cells present - proportional to $q - q_0$ - and the number of cells still to be expected - proportional to $Q - q$ (see fig. 1). Here Q is the maximum amount of dry matter at the end t_e of plant life. q_0 is the dry matter quantity at the moment t_0 that plant life starts, q and t are variates for yield and time respectively. This leads to the formula:

$$\frac{dC}{dq} = \left(\frac{a}{q - q_0} + \frac{1}{Q - q} \right) \quad (5)$$

The assumptions with respect to the shape of the time effect are based on the experience that living organisms often have the disposal of several reaction systems which to a certain extent rule the same process with about the same effect. Here also the reaction should be based on linear relations of the plant physiological time effect T_p to the real cause $t - t_0$ or $t_e - t$.

The basic formula has no need for any adapting functions of the type of formula (3). The formula can be written as:

$$\frac{dT_p}{dt} = \left(\frac{b}{t - t_0} + \frac{1}{t_e - t} \right) \quad (6)$$

This equation states that the plant physiological rate of variation in time is proportional to the age $t - t_0$ and the life expectation $t_e - t$ of the plant.

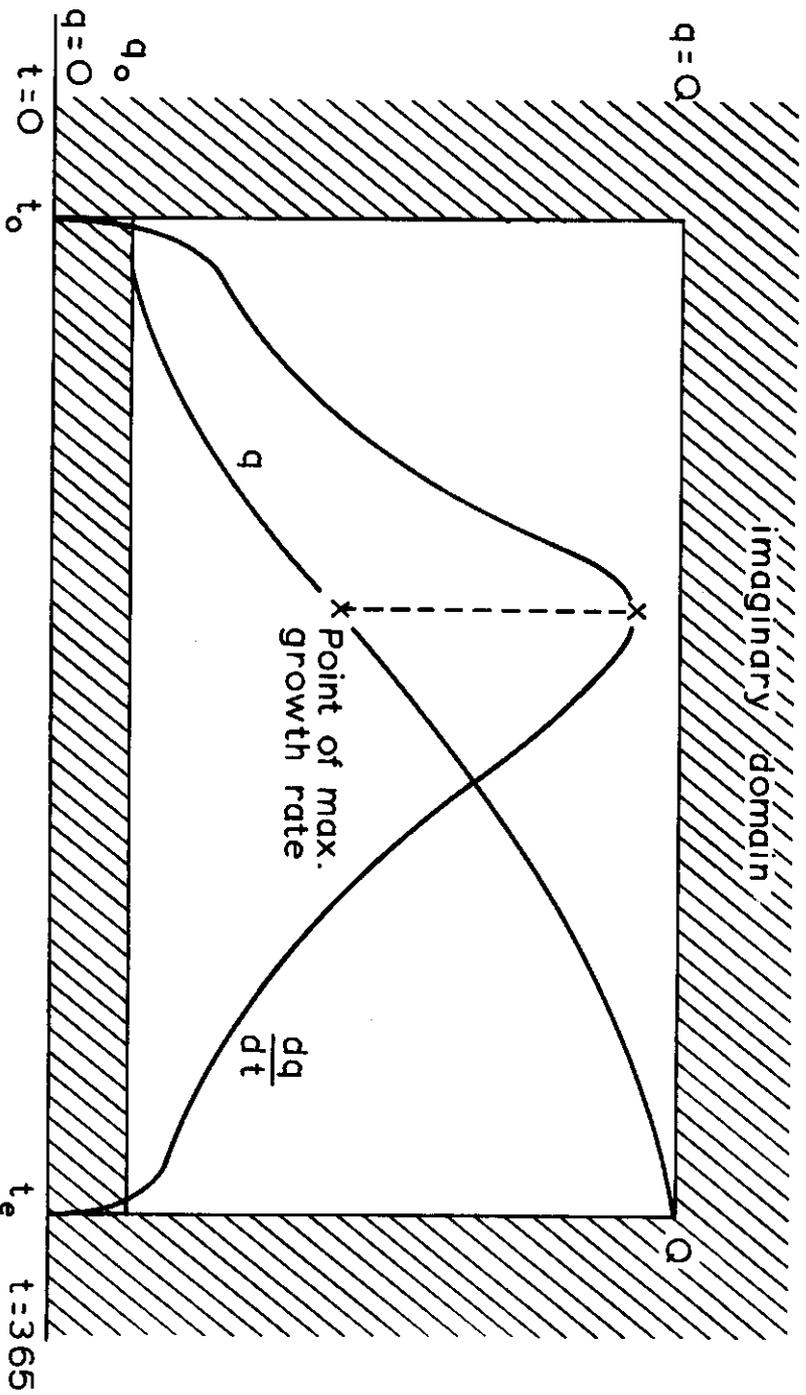


Fig. 1. Significance of the parameters Q , q_0 , t_e and t_0 in the equation for the crop yield q . The four other parameters a , b , c and $\log d$ are less easily indicated but they determine the shape and curvature of the line representing the q - t relation. The other, bell-shaped, curve for the growth rate shows an increasing decline of the growth rate in the neighbourhood of the extremes t_0 and t_e . It is uncertain whether this change in inclination of the line for the growth rate dq/dt points to an incorrectness of the formula or to a plant physiological change in the rate of the processes of life at germination and death of the plant

Special reactions to time

According to formula 4 the formulae 5 and 6 can be combined into a single equation for the relation between the effect t of time and dry matter production q in an additive way as indication of their mutual independency.

The formula reads:

$$\left(\frac{a}{q-q_0} + \frac{1}{Q-q} \right) dq = c \left(\frac{b}{t-t_0} + \frac{1}{t_e-t} \right) dt \quad (7)$$

Integration gives:

$$a \ln (q-q_0) - \ln (Q-q) = \ln d + bc \ln (t-t_0) - c \ln (t_e-t) \quad (8)$$

Equation (8) can also be written as:

$$\frac{(q-q_0)^a}{Q-q} = d \left[\frac{(t-t_0)^b}{t_e-t} \right]^c \quad (9)$$

One may require that the time - yield function represents the peculiarities of the reaction of the plant in such a shape as the reactions are experienced or expected to be inreality. Such expectations are based on the concept of plant response as derived from the combined experience of plant physiological research.

Two questions arise. By adjustment research it has been proven that the 8 parameters, which have to be solved if formula 9 is applied, cannot be solved from 8 observations. The combined values of t_0 and q_0 or t_e and Q drift along the t - q curve during the adjustment without arriving at a fixed value. Equation (9) is apparently too flexible. A further condition should be defined to decrease this flexibility, other than the assumption which is now in use that $b = 1.000$.

The second point deals with the fact that the growth equation may be constructed in such a way that near the beginning date t_0 and the end date t_e the growth rate dq/dt is zero, but it is also possible to choose an equation for which at these points the growth rate - if extrapolated to zero - has a positive finite value. In fig. 2 the extrapolated value at high t -values is $dq/dt = 0.055$ and in fig. 3 $dq/dt = 4$ kg/day. At both ends of plant life a rather sudden change in growth

rate exists. It is most acceptable to assume that it is inherent to life that below a minimum rate of the processes of growth no life is possible. The assumption, leading to equation 11, that life is already possible when the rate of the processes is only little removed from zero is less acceptable.

Comparison with existing formulae

Three equations are to be discussed, of which the exponential curve - equation 10 - and the logistic curve - equation 11 - are generally accepted as useful approximations for the growth relation.

The exponential curve is given by:

$$\frac{dq}{q} = a dt \qquad \frac{q}{q_0} = e^{a(t-t_0)} \qquad (10)$$

For different ascending values of t and q the following results are obtained:

Table 1

t	q	dq/dt	q	t	dq/dt
$-\infty$	0	0	$-\infty$	imag.	imag.
t_0	q_0	$a q_0$	q_0	t_0	$a q_0$
t_e	$q_0 e^{a(t_e-t_0)}$	$a q_0 e^{a(t_e-t_0)}$	Q	$t_0 + \frac{1}{a} \ln \frac{Q}{q_0}$	aQ
$+\infty$	$+\infty$	$+\infty$	$+\infty$	$+\infty$	$+\infty$

The equation gives over the whole range of $t = -\infty$ tot $t = +\infty$ real values for q and dq/dt . Plant physiologically speaking a yield higher than Q makes no sense, a condition not expressed by formula 10. Furthermore the growth rate at the death of the plant with $t=t_e$ is found to be the highest value in plant life. This rapid growth to the moment of death does not agree with the concept of plant growth. Each negative value of q makes the value of t and dq/dt imaginary. Also negative values of q have no plant physiological meaning.

The logistic equation reads:

$$\left(\frac{1}{q} + \frac{1}{Q-q}\right) dq = a dt \qquad \frac{q}{Q-q} = \frac{q_0}{Q-q_0} e^{a(t-t_0)} \quad (11)$$

Here the relation between t and q or t and dq/dt varies as follows:

Table 2

t	q	dq/dt	q	t	dq/dt
$-\infty$	0	0	$-\infty$	imag.	imag.
t_0	q_0	$\frac{aq_0(Q-q_0)}{Q}$	q_0	t_0	$\frac{aq_0(Q-q_0)}{Q}$
t_e	$\frac{q_0 Q e^{a(t_e-t_0)}}{(Q-q_0)+q_0 e^{a(t_e-t_0)}}$	$\frac{aq_0 Q e^{a(t_e-t_0)}}{(Q-q_0)+q_0 e^{a(t_e-t_0)}}$	Q	∞	0
$+\infty$	Q	0	$+\infty$	imag.	$-\infty^2$

Equation 11 gives real values for q in the range for $t = -\infty$ and $t=t_e$. For q the range of real values for t is from $q = 0$ to $q = Q$. The growth rate in this same interval of t starts and ends at zero and passes through a maximum at $q = Q/2$.

A third equation to be used is equation 9. Here the values of q , t and dq/dt all become imaginary below q_0 or above t_e . The same holds for the values of q becoming imaginary below q_0 and above Q .

While in the logistic function an imaginary domain is present at the upper and lower range of q , in equation 9 this imaginary area comprises the upper and lower range of q as well as of t .

Several points seem to plead strongly in favour of equation 9. In the first place the linear relations between crop response and basic plant physiological reactions, as defined in the equations 5 and 6, agree with what is expected on plant physiological grounds. Further, it is in favour of this working hypothesis that no real crop response can be calculated in the imaginary domain outside the square with sides at $t_0 \leq t \leq t_e$ and at $q_0 \leq q \leq Q$.

As a further favourable property is to be considered that the processes of life begin and end as soon as the growth rate has attained a certain positive value. That life only ends if one of the functions of life approaches zero is not a very satisfactory condition. It seems a more convincing supposition that life is not possible if the process activities descend below some characteristic positive finite value.

As most convincing it is to be considered, that imaginarity is found to represent a good indication for non-existence of life. What biologically is impossible should also be mathematically impossible. The impossibility to arrive at real values for plant response by applying a beneficial growth factor if the starting point is imaginary, is an indication for the uniqueness of life.

Significance of derivatives to check yield functions

Formula (9) shows how the yield function is based on the assumption that the growth process is determined by the time elapsed after germination and by the dry matter quantity produced in that time. Further, growth as well is determined by the time during which growth and a dry matter production are till ripening still to be expected.

The equation can be checked and its properties adjusted or clarified and brought into agreement with the biological concept of growth by calculating the derivatives.

These derivatives are expressed by:

$$\frac{dq}{dt} = \frac{Ft}{-Fq}$$

$$\frac{d^2q}{dt^2} = \frac{Ftt + Fqq \left(\frac{Ft}{Fq}\right)^2}{-Fq}$$

$$\frac{d^3q}{dt^3} = \frac{Fttt + 3 Fqq \left(\frac{Ft}{-Fq}\right) \left\{ \frac{Ftt + Fqq \left(\frac{Ft}{Fq}\right)^2}{-Fq} \right\}}{-Fq}$$

In these equations the different symbols stand for:

$$Fq = \frac{a}{q-q_0} + \frac{1}{Q-q} \qquad Ft = \frac{-bc}{t-t_0} - \frac{c}{t_e-t_0} \qquad Ftq = 0$$

$$Fqq = \frac{-a}{(q-q_0)^2} + \frac{1}{(Q-q)^2} \qquad Ftt = \frac{bc}{(t-t_0)^2} - \frac{c}{(t_e-t)^2} \qquad Fttq = 0$$

$$Fqqq = \frac{2a}{(q-q_0)^3} + \frac{2}{(Q-q)^3} \qquad Fttt = \frac{-2bc}{(t-t_0)^3} - \frac{2c}{(t_e-t)^3} \qquad Ftqq = 0$$

(13)

The values of Ftq, Fttq and Ftqq equal zero. The equation for dq/dt is split up in a numerator Ft, function of t alone, and a denominator Fq, a function of q alone. By differentiating the function of t to q and of q to t the derivatives become zero.

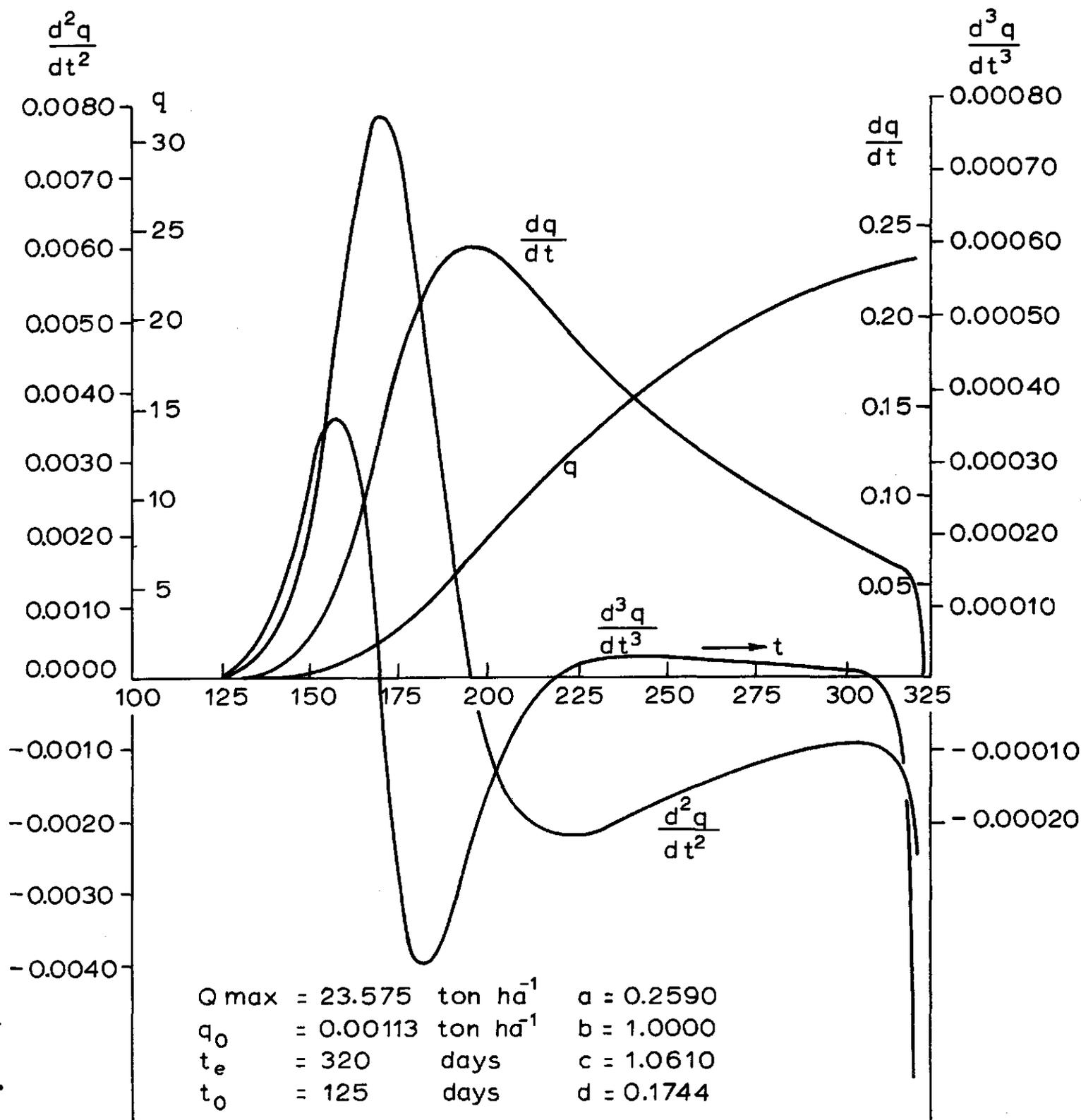


Fig. 2. The properties of the yield curve can be derived from the curves for the successive derivatives. A point of consideration is encountered in the second maximum of the second derivative from a certain experiment with sugar beets at $t = 303$ days. The presence of such a maximum does not seem to follow clearly from the concept of plant growth.

In fig. 2 the shape of the curves for the derivatives and the yield function is given. The curve for q shows that for sugar beets the S-shape is less marked than often is thought. This is due to the fact that for practical purposes the upper part ends in an inclined line, instead of the often expected horizontal one. The curve does not asymptotically approach the horizontal line for $q = Q_{\max}$ and $t = t_e$. The same holds for the combination t_0 and q_0 .

The curve in fig. 2 for the first derivative dq/dt shows that the q - t line starts nearly horizontally but ends inclined. Other sets of calculated data - see fig. 3 - showed that also at low q -values the dq/dt function practically ends with a finite value larger than zero. If the curve is calculated for values of t near to t_0 and t_e it appears that in the first and last few days the inclination changes and dq/dt theoretically approaches zero. But in this small interval yield data are very scarce and checking on available observations will seldomly be possible.

At the intersection of the second derivative with the horizontal axis the flex point of q , the maximum of the growth rate dq/dt , or the zero point of the second derivative d^2q/dt^2 are all found at the 196th day of the year. But the second derivative unexpectedly possesses a second lower maximum at the 303rd day. This second maximum does not seem to agree with the plant physiological concept. It seems more in line with the experience on plant growth to expect that this second maximum would approximately coincide with the upper limit t_e for the growth, which upper limit t_e was the result of an adjustment calculation and was determined as being situated on the 320th day of the year.

If one remembers here the experience that during adjustment Q and t_e tend to drift away and adjustment does not end in a fixed minimum error, then one should conclude that formula 9 is too flexible. By adding a further appropriate relation the flexibility can be curtailed. This condition should consist of a relation between a , Q and t_e . One would expect that by adjustment a relation could be found that would have as effect that for q near to Q and for t near to t_e a fixed point can be calculated where the error is at a minimum.

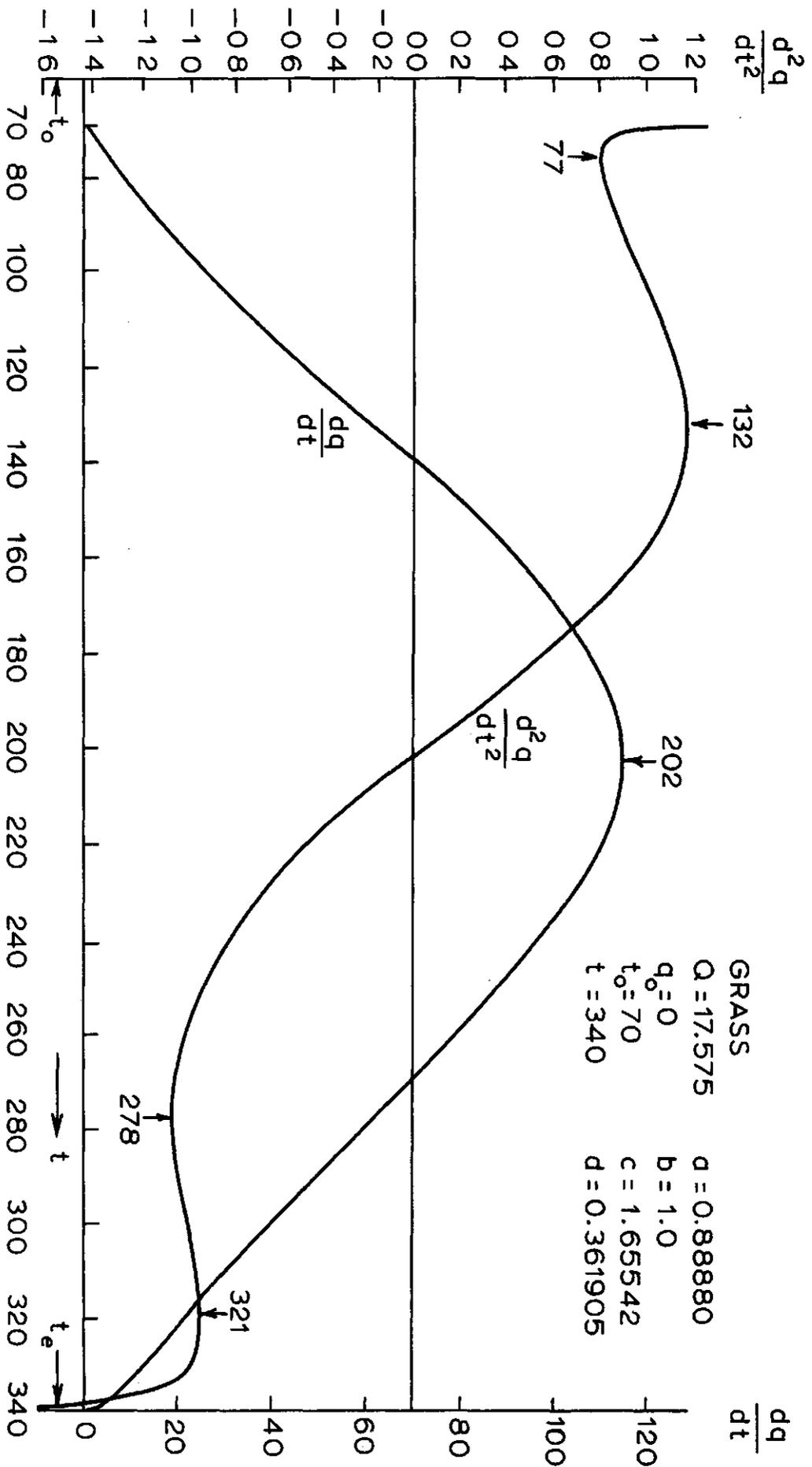


Fig. 3. The maximum of the second derivative at high values of t has its counterpart in a minimum at low t -values. For grassland the two optima are situated at $t = 77$ and $t = 321$ days. This is therefore 7 days after the grass association gives at t_0 the first indication of growing and 19 days before its growth ends at t_e .

The third derivative might represent such a relation by which for $q = Q - \Delta q$ and $t = t_e - \Delta t$ the value of Δq and Δt both approach zero. The accuracy of the adjustment might be highest where the third derivative is zero and the value of t nearly coincides with t_e .

The explanation that the time difference between t_e and the value of t for the second maximum of the third derivative might be the result of the gradual dying of the plant, which would start at the second maximum and in this case for sugar beets lasted therefore 17 days, seems not to be sufficiently convincing. Too many different functions seem to be attributed to a single mathematically defined process.

The value of t and q for the coincidence of $(d^3q/dt^3)_{\max}$ with t_e has to be given as $t_e - \Delta t$ and $Q - \Delta q$ because all derivatives become indeterminate for t equal to t_e and Q . Therefore Δt and Δq should differ from zero.

The description for the time - yield function, which allows all parameters to be solved and which complies with the plant physiological concept of growth, therefore is, if the reasoning about the indication given by the third derivative might prove to be right, probably defined by the following two conditions:

$$\frac{dq}{dt} = c \left[\frac{\frac{b}{t-t_0} + \frac{1}{t_e-t}}{\frac{a}{q-q_0} + \frac{1}{Q-q}} \right] \quad \frac{d^3q}{dt^3} = 0 \quad \text{for} \quad \begin{array}{l} t = t_e - \Delta t \\ q = Q - \Delta q \\ \text{and} \\ t = t_0 + \Delta t \\ q = q_0 + \Delta q \end{array} \quad (14a) \quad (14b)$$

This expansion of the equation for plant growth, defined by these two conditions has up to now not been worked out. As follows from fig. 2 and 3, the effect of formula (14b) on yield and growth rate is very small and in application a sufficient accuracy in the determination of q_0 and Q is obtained by inserting the time of sowing and of ripening in formula (8) or (9) by assuming that $b = 1.00$. For perennials and for plant associations as grass, where the start and finish of growth is not well-defined, a clearer insight in the mathematical representation of the law of plant growth by the use of equations (14a) and (14b) may be of more importance.

Influence of temperature

For perennials, also for other reasons a further expansion of the theory is necessary. In the exponential and the logistic formula, as well as in formula (9), no growth rate equal to zero is possible within the range between t_0 and t_e . In formula (9) even a growth rate zero cannot exist at all because at that value of q the imaginary domain is reached. Still, a zero growth rate must on plant physiological grounds be possible in the mathematical representation. This zero growth occurs during a cold spell and stops plant growth at some arbitrary date. Here a zero growth does not cause the growth process to enter the imaginary domain. This would entirely derange the computation of further growth.

It is habitual to assume that the influence of temperature works by way of the temperature sum. This temperature sum $\sum \tau - \tau_b$ can be considered as a plant physiological time scale T , built up from the real time t , corrected for the temperature τ , as well as the age and life expectancy of the plant. To this end the plant physiological time T is represented by:

$$T = (\tau - \tau_b) \Delta t \quad (15a) \quad T = \sum_{t=0}^i (\tau_t - \tau_b) \quad (15b)$$

τ_b is the temperature at which the process comes to a stop due to the cold climate.

If formula (15b) is applied in formula (6), then this results in:

$$\frac{dT_p}{dT} = \left(\frac{b}{T - T_0} + \frac{1}{T_e - T} \right) \quad (16)$$

For application T is calculated for the full year according formula (15b) so that for each day as well as for specially selected moments as t_0 and t_e the value of the time, weighted for temperature, is available.

Formula (14a) for dq/dT becomes:

$$\frac{dq}{dT} = c \left[\frac{\frac{b}{T-T_o} + \frac{1}{T_e-T}}{\frac{a}{q-q_o} + \frac{1}{Q-q}} \right] \quad (17)$$

If the temperature difference ($\tau - \tau_b$) becomes negative, T has to be taken zero in the calculation. Mathematically this is not difficult or complicated. A plant physiological definition in mathematical terms is less easy. Up to now no formula for the plant physiological time T has been devised, which for positive values of $\tau - \tau_b$ is nearly proportional to the temperature sum, and for negative values renders a value of the plant physiological time T equal to zero. Further the equation should also in this case be built up from linear functions of the real time t and the real temperature τ .

Exponential functions possess these properties of near linearity at high values of the variate and an approximation to zero at low values. Up to now no endeavour was made to fit these mathematical solutions into the concept of plant response. Temperature affects nearly all growth factors and accounting for temperature in only one of them requires careful consideration of the meaning of the parameters calculated. For practical reasons an acceptable solution has to be found without having to elaborate the temperature effect for dozens of other growth factors.

Summary

The plant reacts on a large number of growth factors. The reaction patterns are identical for many growth factors, although the growth parameters may vary.

Several of these growth patterns were already devised earlier (VISSER, 1968; 1969). In this article the specific growth pattern for the factor time was worked out. This time factor, as all other growth factors, has to comply with some special conditions as well as with general conditions.

Plant growth depends on the ratio of the growth rate for all factors combined, as well as the growth rates due to a single factor.

These two growth rates should be as nearly equal as possible. This leads to an optimization which by integration renders formula (1). This formula has the same properties as the yield model of Blackman (BLACKMAN, 1905). This Blackman model is proved to be identical to the result of the assumption that nutrient uptake occurs by means of diffusion.

The growth rate due to a single factor depends on the process according which the factor stimulates plant growth. This effect is in principle proportional to the quantity or the concentration, or any other simple linear relation between the growth factor and the plant response, see formula (2). If the relation is more complicated - as represented in formula (3) - this proves that the quantitative value of factor u is not the active quantity but a related value dependent on the real value x according some intercalated function. Non - linearity within the diffusion-based growth equation shows that other functions are involved resulting from causes working indirectly.

The plant may respond in several different ways. This response is not restricted to dry matter production, but may also involve growth rhythm, the frequency of occurrence of species, the quality of the yield or health of the plant. It may be assumed that within the growth equation these factors are not interrelated. This means that only a relation via a third influence may exist. The reactions can then be linked together additively.

In the actual process of growth of the plant special levels and points occur which have a basic significance. These points and levels should also be represented in the growth equation. No yield can be lower than zero or higher than the maximum yield. No growth is possible before the plant is sown or after the plant dies. These boundaries of growth cannot be represented by a growth rate equal to zero. It is far more acceptable that any plant response outside these two limits t_0 and t_e becomes imaginary. A zero growth can change from one day to the other into a resumed growth. An imaginary growth cannot.

The equation which is developed, has the property of combining the lower limit for the growth rate as well as the limit for the length

of the growth period with the change - over to the imaginary domain for yield and time. Zero yields are not possible in this equation.

Perennial plants in a cold spell, however, show intervals with zero growth which are not combined with a change - over to imaginarity. This growth pattern is of importance if temperature has to be accounted for. By inserting a variable temperature in formula (7) an exact integration is not possible because of the random variation in temperature. The temperature is therefore inserted in formula (17) as the temperature sum, as defined in formula (15b). The integration of formula (17) has to be done numerically. The temperature sum has proved in the past to give a good representation of the time - temperature effect.

The conditions and considerations as described in the formulae (14a), (14b) and (15b), together lead to the definition of plant growth as depicted in formula (17) in which time and temperature are accounted for. Eventually it might become obvious that the condition rendered in equation (14b) might prove to be a valuable amendment. The research to this end, however, has not yet been finished.

Formula (17), whether or not combined with the condition of formula (14b), is a description of the special yield problem for time and temperature, to be inserted in the general description of formula (1b). In general it will be advisable to split up the equation into a time dependent part, to be numerically integrated, and a part treating the growth factors as time independent influences. One should not think lightly of the difficulties that have to be overcome in a correct, multi-factorial elaboration of the yield function.

It appears that the second derivative possesses for sugar beets a double optimum for q at $t = 196$ and 303 days. The second optimum does not seem to comply with the biological concept of plant growth. Further it was found by adjustment of the parameter values that the elaborations for t_e and Q do not lead to a fixed solution. The two parameters keep on drifting to higher values. It should be considered to combine these indications of the existence of a second optimum and the difficulties with the adjustment. The expectation is that the relations between b , Q and t_e , obtained by making the third derivative equal to zero for t near t_e and for q near Q , might

represent a further condition for a correct definition of the model of plant growth. It would mean that only in the last small range Δt of the growth period an increasing decrease of the growth rate will be considered acceptable from a plant physiological standpoint - see fig. 3, the curve for d^2q/dt^2 at high values of t .

As the effect of adjustment according formula (14b) is of slight practical significance, the usefulness of the latter condition has not been given a closer study. In case of adjustment of inaccurate observations, it still might prove to be of sufficient importance to account for the time span between t_e and the time at which the zero value of the third derivative occurs.

It is of considerable importance that from these equations the parameters are calculated by adjustment methods. Adjustment of parameters in cases where different numerical integrations have to be carried out becomes very time consuming, however, It seems advisable to split up the model into parts containing only a single numerical integration and adjust in these part-solutions the parameter values. The integration of these preconstructed parts can then be carried out with the common less accurate simulation methods.

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