NOTA 780   november 1973

Instituut voor Cultuurtechniek en Waterhuishouding
Wageningen

MATHEMATICAL REPRESENTATION OF THE EFFECT

OF SIMULTANEOUSLY OPERATING GROWTH FACTORS

W. C. Visser and P. Kowalik

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de conclusies echter van voorlopige aard zijn omdat het onderzoek
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Bepaalde nota's komen niet voor verspreiding buiten het Instituut
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CONTENT

MATHEMATICAL REPRESENTATION OF THE EFFECT
OF SIMULTANEOUSLY OPERATING GROWTH FACTORS

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Importance of complete plant response models

A mathematical representation of the effect of growth factors
on plant yield or growth rate is of importance for several reasons.
Such a model could be used to calculate what human intervention in
soil fertility or moisture conditions would have the largest desirable
effect. Or the determination of a number of soil properties or hydro-
logic constants could be aimed at. If these soil properties were de-
termined in the laboratory and - for instance in pot trials - the plant
parameters were also assessed, then a simple calculation could
show, what the yield increase would be as a result of improvement
of one or more productivity factors.

A computer model of plant response could also be used to de-
termine constants as it would be possible to assess parameters for
the physical properties of soils, of plants or of plant associations.
The mathematical model in this way could become a substitute for
the laboratory. Such an indirect, mathematical determination of
parameters would be less costly than the direct determination in
the laboratory or glasshouse. This is particularly to be expected if
the number of constants becomes somewhat larger.

Determinations by means of calculation present still another
advantage. A formula nearly always is an approximation. The para-
meters with which an acceptable result with such a formula is ob-
tained, will differ from the values obtained in the laboratory. If ad-
justment techniques are used, the general result of the model would
be as near to the observed value as observational errors allow. An

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error in a model can be made good by a compensating error in the calculated constants. In such cases the parameters are in error, but the result as yields and growth rates, calculated with the parameters inserted in the model which was used for assessing the parameters, would be influenced only in a minor way by the shortcomings of the model. One error would be compensated by another.

A description of the existing soil fertility situation by means of the result of the model could be condensed to a soil fertility classification and could be used to advise farmers on the need for fertilizer application or hydrologic improvement. The above mentioned aspects are all of mainly practical importance.

The scientific importance of the complete plant response model also should be stressed, however. Up to now research is carried out according the principle of changing one factor and keeping all others constant. In fact the other factors generally are neglected.

A model will enable one to insert the other factors into the mathematical elaboration initially in an approximate way. What is known about the reaction of a crop to a growth factor, even if it is of a restricted accuracy, will soon allow to increase the accuracy more than would be attained by omitting such factors. It is probable that the research philosophy of the ceteris paribus principle better should be rejected because it lost its necessity. A computer is able to account for many factors at the same time, so simplification by omitting factors is not needed any more. The research philosophy should shift more and more to the panta rei principle in which every factor may vary and is acting according to its level of intensity.

When using the panta rei principle one gets an impression of the magnitude of the effect of each soil property. This will stimulate to study first the quantitatively most important factors.

The conceptual basis of the model here presented

It is often not easy to understand, what may be the reason that a yield is higher or lower than was expected. In plant response, however, there is a certain system which, when used correctly, makes understanding easier.

Crop yield is the result of a large number of simultaneously operating growth factors. The effect of various factors has a part in common because all these effects are based on the same principle of nutrient uptake. This principle will be called the general relation. Partly the effects will differ because they are related to a special cause for each factor. This will be called the special relation. By reflecting on the how and why of the magnitude of the yield, the distinction between the general and special reactions can be helpful in arriving at a correct understanding.

So one rather often observes that it is expected that expressing the yield as a percentage of some maximum yield will simplify the representation of productivity relations. The mathematical representation of the yield, divided by some maximum yield is only acceptable, however, if the growth relation contains functions of a procentual yield q/q_o. This is only the case with the exponential yield equation and the Cobb Douglas relation, as used by HOMES (1966). But these formulae are nog generally valid. For the MITSCHERLICH equation (1925) one better could use the procentual relation of the yield deficit $(Q-q)/(Q-q_o)$. The Blackman principle (BLACKMAN, 1905) gives the largest simplification if the yield - growth factor curves are shifted in such a way that the oblique asymptotes coincide. Here no procentual relation is valid but an additive relation.

The simplification of the graphical representation of the yield data gives the best results, when the simplification in a well considered way follows closely the mathematical representation.

The problem of mathematical representation of simultaneously operating growth factors should be based on carefully determined physically acceptable functions for the special relation for all separate growth factors involved, as well as on a generally valid plant physiological function for the general relation.

The general and special growth functions

The general relation for the growth function can best be based on the diffusion equation. This general relation is represented by (VISSER, 1969):

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

The special equation for each growth factor separately can be represented in its simplest shape by:

$$q_x = a(x-x_0)$$

$$q_y = b(y-y_0)$$

q = actual yield
q_x, q_y = theoretical yield for x, y
Q = maximum yield
a, b = growth parameters
F = flexibility constant $\hspace{1em}$ (2)

Inserting formula (2) in formula (1) leads to:

$$\left(1 - \frac{q}{Q}\right)\left(1 - \frac{q}{q_x}\right)\left(1 - \frac{q}{q_y}\right) \cdots = F \tag{3}$$

The maximum yield Q is the largest productivity to which the plant on biological grounds is able to yield or the one that is due to the limiting activity of an unknown growth factor. The flexibility factor F expresses within what range of ratios of absorbed nutrients unhampered growth is possible.

If the ratio between the nutrients was strictly fixed and for n parts of nitrogen the plant absolutely would need p parts of potassium and f parts of phosphate, then the flexibility factor F would be zero. A healthy growth is possible, however, when these ratios vary within certain limits. This flexibility is represented by a small value for F. By using adjustment techniques a small positive value is found.

This flexibility is graphically indicated by the vertical distance between the yield curve q and the intersection point I for the two asymptotes of the type $q_x = a(x-x_0)$ mentioned above. This is represented in fig. 1.

If a larger number of growth factors than two is involved, the vertical distance in fig. 1 is no longer equal to the square root of F/Q, but to a higher root corresponding to the number of factors of which the asymptotes intersect.
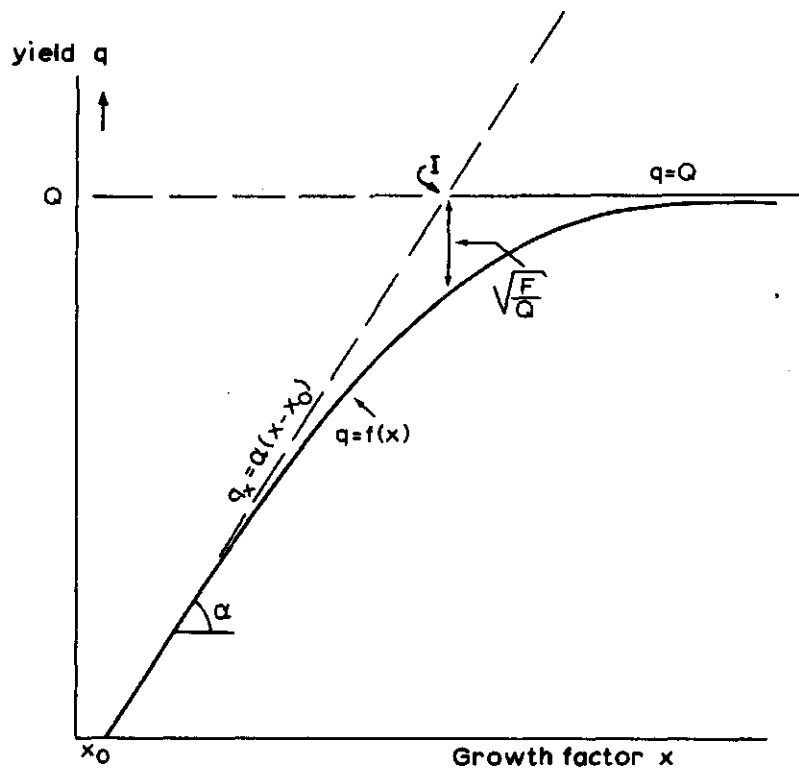
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Fig. 1. The yield curve q is determined by two asymptotes. One for the maximum yield q = Q and one for the growth factor dependent asymptote $q = a(x-x_o)$. The flexibility parameter F depends on the vertical distance between the yield curve q and the point of intersection of the asymptotes I

Equations for special types of response

The special equations given in formula (2) are the least complex linear cases. In growth equation (3), however, also non-linear relations can be inserted. These equations of a more complex nature are described elsewhere (VISSER, 1968; 1969).

Different types of models have been constructed, for instance the cooperation to a combined effect of the partial effects of different intensities of the same factor in successive layers of the soil profile. Other somewhat complicated relations sometimes result from antagonistic connections between factors. It also will be of importance to use models which account for storage of nutrients in the plant, which storage is depleted if the stock of nutrients in the soil becomes insufficient.

As not all relations have been described in models an investigation in the shape of the type of special relations which occur in nature is needed to close the existing gap in the knowledge on soil fertility and plant production. It is not to be expected that a comprehensive operational model in the form of a mathematical representation of plant response to be used in practical application, is already possible.

A type of model with considerable importance is the model that contains the time - yield relation together with other eventually limiting factors. For each factor it sometimes may be necessary to account for variations in its level of intensity during the growth period. Intervention in the fertility level of a field not only requires a decision about the magnitude of the intervention but also about the moment of the year at which the change in intensity of the growth factor should be carried out.

The equation for the response to time

The factors which vary with time will often differ in an irregular way, like rainfall or evaporation. Such influences cannot be described by an exact integral over time, but have to be integrated numerically. To make this possible the equation should not be evolved for yield q but for growth rate dq/dt. This derivative shall be indicated by $\dot{q}$.

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The formula for the growth rate is given by the equation:

$$\left(1 - \frac{\dot{q}_L}{\dot{q}_{nLT}}\right)\left(1 - \frac{\dot{q}_L}{\dot{q}_y}\right)\left(1 - \frac{\dot{q}_L}{\dot{q}_z}\right)\left(1 - \frac{\dot{q}_L}{\dot{q}_u}\right) \ldots = F \qquad (4)$$

The index nLT indicates that the non-limiting (nL) special equation, expressed as growth rate, holds for the factor time expressed as temperature sum T. The indexes y, z, u, ... indicate other factors as aeration and evaporation. Further $\dot{q}_L$ indicates the actual growth rate under influence of limiting (L) or non-limiting (nL) additional factors.

The magnitude of $\dot{q}_{nLT}$ can be calculated with a formula of which the solution is discussed elsewhere (VISSER, 1974). The solution for $\dot{q}_{nLT}$ is:

$$\dot{q}_{nLT} = c \;\frac{\dfrac{b}{T-T_o} + \dfrac{1}{T_e-T}}{\dfrac{a}{q-q_o} + \dfrac{1}{Q-q}} \qquad (5)$$

a, b, c = constants
q_o, Q = dry matter yield at beginning, end
T_o, T_e = temperature sum at beginning, end
q, T = variable dry matter yield, temperature sum
$\dot{q}_{nLT}$ = theoretical non-limited daily yield increase for time - temperature factor

The expression of $\dot{q}_{nL}$ by functions of T and Q

The value of $\dot{q}_{nLT}$ is expressed as a function of the time variant Q and has to be defined as a function of a constant value or of a value already known from the calculation results for a previous day in the day-to-day numerical solution. The solution was reconnoitered first by solving the $\dot{q}_{nLT}$ from an equation similar to (5) in which a and b were taken as unity to simplify the elaboration.

The equation with which was started, is:

$$\left(\frac{1}{q-q_o} + \frac{1}{Q-q}\right) dq = c \left(\frac{1}{T-T_o} + \frac{1}{T_e-T}\right) dT \qquad (6)$$

This can be written as:

$$\frac{dq}{dT} = c \, \frac{(T_e - T_o)(q - q_o)(Q - q)}{(Q - q_o)(T - T_o)(T_e - T)} \tag{7}$$

Integrating formula (6) and solving for q, yields:

$$q = \frac{q_o + PQ}{1 + P} \quad \text{with} \quad P = d \left(\frac{T - T_o}{T_e - T}\right)^c \tag{8}$$

With formula (8) the terms $(q - q_o)$ and $(Q - q)$ can be expressed and inserted in formula (7):

$$\frac{dq}{dT} = \frac{cP}{(1 + P)^2} \, \frac{(T_e - T_o)}{(T - T_o)(T_e - T)} \, (Q - q_o) \tag{9}$$

This was condensed to:

$$\frac{dq}{dT} = D(Q - q_o) \tag{10}$$

In equation (10) D is a function of T alone. This solution for a simplified equation now can be used to direct the solution from a more complicated one.

Solution of $\dot{q}_{nLT}$ for the more complicated equation

The technique that led to formula (10) for $a = b = 1$ can be applied to formula (5) with values for a and b differing from unity. This is done by writing for formula (5):

$$\dot{q}_{nLT} = D(Q - q_o) = g \, \frac{\dfrac{b}{T - T_o} + \dfrac{1}{T_e - T}}{\dfrac{a}{q - q_o} + \dfrac{1}{Q - q}} \qquad g = \text{time dependent parameter} \tag{11}$$

In this equation two values are unknown, the values of D and Q, both functions of T. These D and Q are solved in the next chapter.

Influence of time on the maximum yield Q_i

The influence of a growth factor on the plant yield is a cumulative one. The yield at successive days can be described by:

$$q_{T+1} = q_T + \dot{q}_{T+1} \tag{12a}$$

$$q_{T+n} = q_T + \sum_{i=T}^{T+n} \dot{q}_i \tag{12b}$$

The yield at some moment i of the growth period follows from the maximum yield Q_{max} at the time - temperature sum T_e of which is subtracted the difference between the unhampered yield q_{nLi} minus the limited yield q_{Li} on the same day

$$Q_i = Q_{max} - (q_{nLi} - q_{Li}) \tag{13a}$$

and for the previous day

$$Q_{i-1} = Q_{max} - (q_{nLi-1} - q_{Li-1}) \tag{13b}$$

subtraction produces:

$$Q_i - Q_{i-1} = (q_{Li} - q_{Li-1}) - (q_{nLi} - q_{nLi-1})$$

$$Q_i - Q_{i-1} = \dot{q}_{Li} - \dot{q}_{nLi} \tag{13}$$

Inserting equation (11) in (13) leads to:

$$Q_i - Q_{i-1} = \dot{q}_{Li} - D_i(Q_i - q_o)$$

$$Q_i = \frac{\dot{q}_{Li} + q_o D_i + Q_{i-1}}{1 + D_i} \tag{14}$$

A basic assumption has to be made to obtain a solution for the response of a plant to time in relation with the actual yield Q_i which the plant is able to produce. This assumption is, that the decrease in yield due to the limiting effect of some factor will cause a lowering in ultimate yield by the same yield difference that occurs on the day with a deficiency of that factor.

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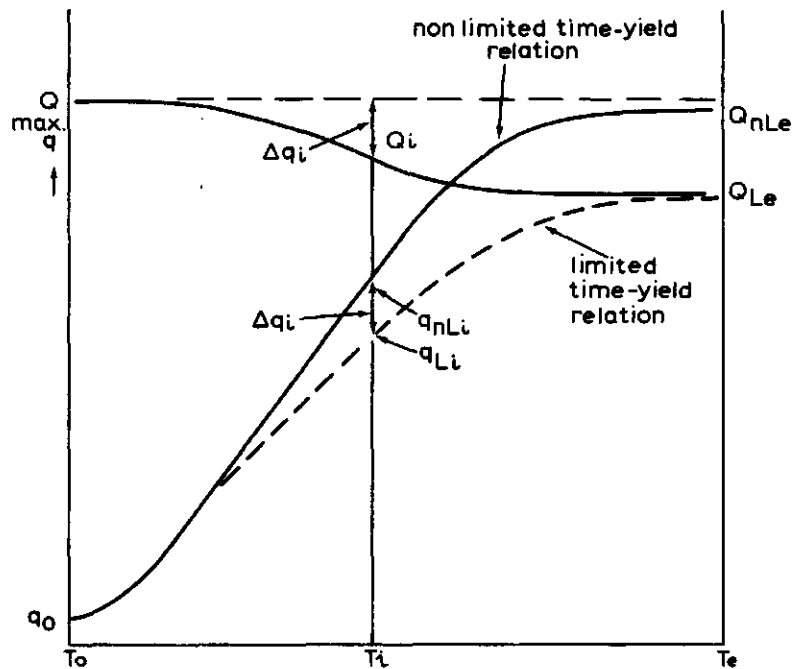
Fig. 2. The formula for the S-shaped course of the yield curve depends according formula (5) on the magnitude of the difference $Q-q$. A limiting factor reducing q increases the value of $Q-q$ and will cause the last part of the curve for the yield q_L to become less steep. This means that Q_{max} for that day is reduced to Q_i. The reduction of Q_{max} to Q_i is equal to the difference in the non-limited yield q_{nLi} and the yield q_{Li} under influence of limiting factors

In fig. 2 this is graphically represented. The difference between Q_{max} and Q_i is equal to the difference of q_{nLi} and q_{Li}, both equal to Δq_i. The magnitude of Q_{max} and T_e is decreased to $Q_{max} - \Sigma \Delta q_i$ as represented in formulae (13a) and (14).

It might be subject for discussion whether a decrease of Q_{max} to Q_i will influence any future $\dot{q}$ according the same $Q - \Sigma \Delta q$ value over the full length $T_e - T_i$ of the time - temperature sum. It might be supposed that a lower number of cells, taking part in the cell division might be compensated for in the further growth period by an increased growth rate. The initial decrease in yield might in that way loose its importance if time progresses.

If one defines the yield q_{nLT}, however, as a yield not affected detrimentally by any growth factor save the time factor, then this yield is the highest possible one which the plant is able to produce. Then no higher growth rate $\dot{q}$ than $\dot{q}_{nLT}$ is possible and it is to be accepted that the yield Q_e will be Δq_e units lower than Q_{max}.

As will be discussed later, however, there is still a possibility that the time effect on yield does not only depend on an effect on the value of Q, but also on the value of q_o. The yield function in which, due to limiting factors, instead of $Q_i - q$ has to be inserted $(Q_i - \Delta_1 q) - q$, can be supplemented by an effect on q_o shaping the $(q - q_o)$ value to $q - (q_o + \Delta_2 q)$ and changing formula (5) to:

$$\dot{q}_{Lt} = c \, \frac{\dfrac{b}{T - T_o} + \dfrac{1}{T_e - T}}{\dfrac{a}{q - (q_o + \Delta_2 q)} + \dfrac{1}{(Q - \Delta_1 q) - q}}$$

$\Delta_1 q = Q_{max} - Q_i$, see fig. 2

$\Delta_2 q$ = yet undefined decrease in production capacity of present cells $(q - q_o)$ due to severe damage

Determination of the time dependent function D

In equation (11) the formula for the non-limited growth rate $\dot{q}_{nL}$ is given. What is aimed at with this formula is to calculate daily values of the limited growth rate $\dot{q}_L$. This can be carried out if D_i is expressed with time independent constants or magnitudes which were already solved for the previous day.

In formula (11) for D_i the following expression was already available:

$$D_i = \frac{\dot{q}_{nLi}}{Q_i - q_o} \tag{11}$$

Inserting formula (13a) in (11) yields:

$$D_i = \frac{\dot{q}_{nLi}}{Q_{max} - q_{nLi} + q_{Li} - q_o} \tag{15}$$

By replacing q_{Li} by $q_{Li-1} + \dot{q}_{Li}$ the formula becomes:

$$D_i = \frac{\dot{q}_{nLi}}{(Q_{max} - q_{nLi} + q_{Li-1} - q_o) - \dot{q}_{Li}} \tag{16a}$$

Simplifying formula (16a) by condensing to

$$Q_{max} - q_{nLi} + q_{Li-1} - q_o = Li \tag{16b}$$

gives the result

$$D_i = \frac{\dot{q}_{nLi}}{Li - \dot{q}_{Li}} \tag{17}$$

Formula (14) for Q_i and (17) for D_i together with formula (4) for $\dot{q}_{Li}$ contain not only the still unknown parameters Q_i and D_i but also $\dot{q}_{Li}$, the value which is finally to be determined for the yield under influence of all factors.

The magnitudes Q_{max} and q_o are given constants. Q_{i-1} is calculated in the day-for-day elaboration for the previous day and is also known. The non-limiting values q_{nLi-1} and q_{nLi} are calculated with formula (11) and numerically integrated. The magnitudes Q_i and D_i are eliminated from formula (4) and $\dot{q}_{Li}$ can be solved.

Solution of the growth rate as influenced by the limiting factors

Each term of formula (4) contains the unknown growth rate $\dot{q}_{Li}$. Only the first term contains $\dot{q}_{Li}$ in the numerator as well as the

denominator and by writing the model as polinomial the n growth factors are combined to a $(n+1)$-degree function of the unknown $\dot{q}_{Li}$.

First Q_i is eliminated:

$$\dot{q}_{nLi} = D_i (Q_i - q_o) \qquad \text{(11, first part)}$$

$$= \frac{D_i}{1+D_i} (\dot{q}_{Li} + D_i q_o + Q_{i-1} - q_o - q_o D_i) \qquad \text{(18a)}$$

$$= \frac{D_i}{1+D_i} (\dot{q}_{Li} + Q_{i-1} - q_o) \qquad \text{(18b)}$$

$$= \frac{D_i}{1+D_i} (k_i + \dot{q}_{Li}) \qquad \text{(18c)}$$

In formula (18b) the term $(Q_{i-1} - q_o)$ is condensed to

$$k_i = Q_{i-1} - q_o \qquad \text{(18d)}$$

The first formula is part of equation (11). Formula (18a) is the result of inserting formula (14) in (11). Here $D_i q_o$ cancels out and leads to formula (18b). If $(Q_{i-1} - q_o)$ is combined to k_i, formula (18c) is obtained. This result is inserted in the first term of equation (4).

$$(1 - \frac{\dot{q}_{Li}}{\dot{q}_{nLi}}) = 1 - \frac{\dot{q}_{Li}}{\frac{D_i}{1+D_i} (k_i + \dot{q}_{Li})}$$

$$= \frac{D_i k_i - \dot{q}_{Li}}{D_i (k_i + \dot{q}_{Li})}$$

$$= \frac{k_i - \dot{q}_{Li}/D_i}{k_i + \dot{q}_{Li}}$$

Insert formula (17) and multiply with $(k_i + \dot{q}_{Li})$ at both sides of equation (4), see formula (20).

$$k_i - \frac{\dot{q}_{Li}}{D_i} = k_i - \frac{Li \, \dot{q}_{Li} - \dot{q}_{Li}^2}{\dot{q}_{nLi}}$$

$$= \frac{k_i \, \dot{q}_{nLi} - Li \, \dot{q}_{Li} - \dot{q}_{Li}^2}{\dot{q}_{nLi}} \qquad \text{(19)}$$

By inserting formula (19) in formula (4) an equation expressing $\dot{q}_{Li} = X$ as a polynomium of the unknown $\dot{q}_{Li}$ is obtained containing further only known magnitudes and values dependent on time.

$$\left[\dot{q}_{nLi}\, k_i - Li\, X - X^2\right]\left[(\dot{q}_{yi} - X)(\dot{q}_{zi} - X) \ldots\right] =$$
$$= \left[\dot{q}_{nLi}\, \dot{q}_{yi}\, \dot{q}_{zi} \ldots \times (k_i + X)\, F\right] \tag{20}$$

It must be noted that as many additional factors as are of quantitative importance can be inserted in equation (20). Only two such factors were mentioned here but the equation for yield or growth rate theoretically is only valid if all existing growth factors are present in it. The minimization on which the equation is based accounts for the minimization of the difference between q_L and q_{nL} for all additional factors.

Evaluation of the growth rate if additional factors are present

The solution of X from equation (20) can be obtained in two different ways.

1. Solution with increasingly improved approximations

A first method is to calculate formula (20) with a few well chosen approximations for X, and see at what value of X the difference between the two products of the terms changes from positive to negative.

The equation is written in the following way to get a first crude approximation of X:

$$\left(\frac{\sqrt{Li^2 + 4k_i\dot{q}_{nLi}} - Li}{2} - X\right)\left(\frac{\sqrt{Li^2 + 4k_i\dot{q}_{nLi}} + Li}{2} + X\right)\left(\dot{q}_{yi} - X\right) \times$$
$$\times \left(\dot{q}_{zi} - X\right) \ldots - \dot{q}_{nLi}\dot{q}_{yi}\dot{q}_{zi} \ldots \times (k_i + X)\, F = 0 \tag{21}$$

The estimate of X will not exceed the value of the constant with the lowest value $\dfrac{\sqrt{Li^2 + 4k_i\dot{q}_{nLi}} - Li}{2}$ or $\dot{q}_{yi}$ or $\dot{q}_{zi}$.

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The value of X will neither be much lower than the value of that constant. Of the $(n+2)$ roots of the equation with n the number of additional factors, the lowest value is valid. A linear interpolation soon produces a sufficiently accurate approximation of the actual growth rate $\dot{q}_{Li}$.

2. Solution with a polynomial

A second method to determine the value of growth rate $\dot{q}_{Li}$ is to follow the well known technique of solving polynomials.

The equation can generally be represented by:

$$E + GX + HX^2 + MX^3 + NX^4 + RX^5 + SX^6 = 0 \tag{22}$$

Further all parameters E to S from equation (22) are of an identical construction

$$P_{ji} = P_{j1} \, k_i \, \dot{q}_{nLi} + P_{j2} \, Li + P_{j3} \tag{23}$$

Here j indicates the number of additional factors which is accounted for. For $j = 1$ only one additional factor is taken up. The formula is constructed for 4 additional factors or $j = 4$. The parameters p_j are built up with a restricted number of combinations of $\dot{q}_y$, $\dot{q}_z$ .... . These combinations will be indicated with α, β, ... The value of q_y will be represented by y, q_z by z .... to abbreviate the description.

If the symbols y, z, ... are placed next to each other as $(y, z \, ..)$ then the n values should be multiplied. If the values are placed above each other, as $\begin{pmatrix} y \\ z \\ \vdots \end{pmatrix}$ they should be added. For α and β a full description as well as the abbreviated representation are given. The index of α and β indicates the number of additional factors.

$$\alpha_1 = y \quad = \left(\dot{q}_y \right)$$

$$\alpha_2 = yz \quad = \left(\dot{q}_y \dot{q}_z \right)$$

$$\alpha_3 = yzu \quad = \left(\dot{q}_y \dot{q}_z \dot{q}_u \right)$$

$$\alpha_4 = yzuw = \left(\dot{q}_y \dot{q}_z \dot{q}_u \dot{q}_w \right)$$

$$\alpha_1 = \beta_1 = \binom{y}{} = \left(\dot{q}_y \right)$$

$$\beta_2 = \binom{y}{z} = \left(\dot{q}_y + \dot{q}_z \right)$$

$$\beta_3 = \binom{y}{z \ u} = \left(\dot{q}_y + \dot{q}_z + \dot{q}_u \right)$$

$$\beta_4 = \begin{pmatrix} y \\ z \\ u \\ w \end{pmatrix} = \left(\dot{q}_y + \dot{q}_z + \dot{q}_u + \dot{q}_w \right)$$

$$\beta_2 = \gamma_2 = \begin{pmatrix} y & 1 \\ 1 & z \end{pmatrix} \qquad \gamma_3 = \begin{pmatrix} y & z & 1 \\ y & 1 & u \\ 1 & z & u \end{pmatrix} \qquad \delta_4 = \begin{pmatrix} y & z & u & 1 \\ y & z & 1 & w \\ y & 1 & u & w \\ 1 & z & u & w \end{pmatrix}$$

$$\beta_3 = \delta_3 = \begin{pmatrix} y & 1 & 1 \\ 1 & z & 1 \\ 1 & 1 & u \end{pmatrix} \qquad \delta_4 = \begin{pmatrix} y & z & 1 & 1 \\ y & 1 & u & 1 \\ y & 1 & 1 & w \\ 1 & z & u & 1 \\ 1 & z & 1 & w \\ 1 & 1 & u & w \end{pmatrix}$$

$$(24)$$

A few combinations are identical. So is $\alpha_1 = \beta_1$, $\beta_2 = \gamma_2$, $\beta_3 = \delta_3$.

In four different ways a simplification and shortening of the presentation of the polynomial was persued. This purpose is served by the p_{ji} representation of formula (23) and the writing of y for $\dot{q}_y$, z for $\dot{q}_z$, further by the combination of the derivatives $\dot{q}_y$, $\dot{q}_z$ ... according formula (24) and the shortened indication X for $\dot{q}_{Li}$.

This renders the following result:

$$(e_1 k_i \dot{q}_{nLi} + e_2 Li + e_3) \quad + (g_1 k_i \dot{q}_{nLi} + g_2 Li + g_3) X +$$

$$+ (h_1 k_i \dot{q}_{nLi} + h_2 Li + h_3) X^2 + (m_1 k_i \dot{q}_{nLi} + m_2 Li + m_3) X^3 +$$

$$+ (n_1 k_i \dot{q}_{nLi} + n_2 Li + n_3) X^4 + (r_1 k_i \dot{q}_{nLi} + r_2 Li + r_3) X^5 +$$

$$+ (s_1 k_i \dot{q}_{nLi} + s_2 Li + s_3) X^6 = 0 \qquad (25)$$

Equation (25) is given for maximally four additional growth factors. The parameters e to s in equation (25) still have to be expressed as functions of α to δ. This relation is given in formula (26) for 1 to 4 additional factors, indicated by the first index 1 to 4. The second index 1 to 3 indicates the position of the parameter in the expression for E to S in equation (23).

$$
\begin{array}{llllll}
e_{11}=+\alpha_1(1-F) & e_{12}=+0 & e_{13}=+0 & g_{11}=-1 & g_{12}=-\alpha_1 & g_{13}=-\alpha_1\dot{q}_{nLi}F \\
e_{21}=-\alpha_2(1-F) & e_{22}=-0 & e_{23}=-0 & g_{21}=+\gamma_2 & g_{22}=+\alpha_2 & g_{23}=+\alpha_2\dot{q}_{nLi}F \\
e_{31}=+\alpha_3(1-F) & e_{32}=+0 & e_{33}=+0 & g_{31}=-\gamma_3 & g_{32}=-\alpha_3 & g_{33}=-\alpha_3\dot{q}_{nLi}F \\
e_{41}=-\alpha_4(1-F) & e_{42}=-0 & e_{43}=-0 & g_{41}=+\gamma_4 & g_{42}=+\alpha_4 & g_{42}=+\alpha_4\dot{q}_{nLi}F
\end{array}
$$

$$
\begin{array}{llllll}
h_{11}=+0 & h_{12}=+1 & h_{13}=-\alpha_1 & m_{11}=-0 & m_{12}=-0 & m_{13}=+1 \\
h_{21}=-1 & h_{22}=-\gamma_2 & h_{23}=+\alpha_2 & m_{21}=+0 & m_{22}=+1 & m_{23}=-\gamma_2 \\
h_{31}=+\delta_3 & h_{32}=+\gamma_3 & h_{33}=-\alpha_3 & m_{31}=-1 & m_{32}=-\delta_3 & m_{33}=+\gamma_3 \\
h_{41}=-\delta_4 & h_{42}=-\gamma_4 & h_{43}=+\alpha_4 & m_{41}=+\beta_4 & m_{42}=+\delta_4 & m_{43}=-\gamma_4
\end{array}
$$

$$
\begin{array}{llllll}
n_{11}=+0 & n_{12}=+0 & n_{13}=-0 & r_{11}=-0 & r_{12}=-0 & r_{13}=+0 \\
n_{21}=-0 & n_{22}=-0 & n_{23}=+1 & r_{21}=+0 & r_{22}=+0 & r_{23}=-0 \\
n_{31}=+0 & n_{32}=+1 & n_{33}=-\delta_3 & r_{31}=-0 & r_{32}=-0 & r_{33}=+1 \\
n_{41}=-1 & n_{42}=-\beta_4 & n_{43}=+\delta_4 & r_{41}=+0 & r_{42}=+1 & r_{43}=-\beta_4
\end{array}
$$

$$
\begin{array}{lll}
S_{11}=+0 & S_{12}=+0 & S_{13}=-0 \\
S_{21}=-0 & S_{22}=-0 & S_{23}=+0 \\
S_{31}=+0 & S_{32}=+0 & S_{33}=-0 \\
S_{41}=-0 & S_{42}=-0 & S_{43}=+1
\end{array}
$$

First index   = number of additional factors
Second index = position in equation (23)

$$(26)$$

A number of the q_y, q_z ... combinations are for four additional factors equal to zero, in case of more than four of these factors they would have obtained a specific value, however. Therefore also when the value is zero, here the sign of the parameter is given in the values in the survey of (26). If more than four additional factors are present, new combinations in survey (24) will have to be worked out, for instance those with five or more columns.

The calculation of $\dot{q}_{Li}$ starts with the determination of $\dot{q}_{yi}$, $\dot{q}_{zi}$ ... The next step is to calculate the combinations α to δ from formula (24). Then with formula (26) the values of e_{11} to S_{13} are assessed and the terms P_{ji} are calculated according formula (23). If the values P_{ij} are known then according formula (25) the value of $X = \dot{q}_{Li}$ is determined. This value of X only holds for the day i. The calculation is to be repeated for all consecutive days with which the investigation deals.

Examples of calculation

By using formula (22) or by obtaining the solution of $\dot{q}_{Li}$ with formula (21) the result for $X = \dot{q}_{Li}$ is calculated for successive values of T. The result is graphically represented in fig. 3. The sum of the values for consecutive days of $\dot{q}_L$ provides the value of q_L.

The graph is made for grassland and it is assumed that the constant additional growth factor y does not allow a growth rate of more than 100 kg $ha^{-1}day^{-1}$. The period over which the limiting influence keeps the growth rate down lasts from the 110th till the 260th day of the year or 150 days.

The two periods at the beginning and end during which the limiting factor exerts no influence, together last 90 days. The 150 days with a growth rate somewhat less than 100 kg $ha^{-1}day^{-1}$ causes a decrease in the ultimate yield of nearly 27500 - 90 x 100/2 + 150 x 100 or 8000 kg. From careful calculations of the growth rate it appears that actually the yield decrease with 7530 kg is somewhat less. The difference results from the assumption in the first calculation of the yield decrease that the curve for plant response is approximated by a curve with a trapezoidal shape.

Influence of the height of the limiting level

The calculation of the growth rate in fig. 3 was carried out for different limiting levels. For this limiting level for $\dot{q}_y$, values were taken of 60 to 500 kg $ha^{-1}day^{-1}$. The non-limiting level for $\dot{q}_{nLT}$, the highest level of $\dot{q}_{nL\,max}$ of the investigation, was found to be about 165 kg $ha^{-1}day^{-1}$.

A point in fig. 4 which requires some attention is the general concept of what is considered being a limiting factor. This proves to be, that if an additional factor only allows a yield level q_y, lower than the productivity q_L of all other operating factors combined, the additional factor is limiting. Has the additional factor such a limiting level that the yield q_y due to this factor alone surpasses the maximum yield q_L of the other operating factors, then the additional factor is considered to exert no influence on the yield.
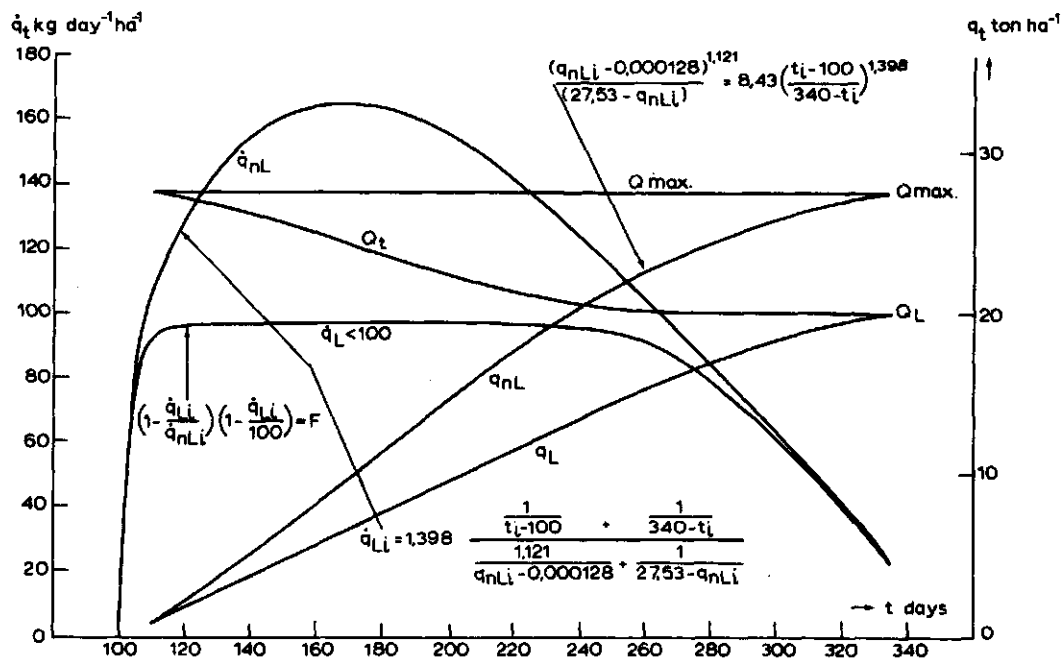
Fig. 3. As long as the growth rate of the plant is lower than the growth rate to which a deficient growth factor would limit a plant, this rate is determined by the age of the plant. Only when the time dependent growth rate $\dot{q}_{nLi}$ is larger than the factor dependent growth rate $\dot{q}_{Li}$ the velocity of the growth is reduced by the introduction of such a factor. The sum of the growth rates determines the yield q_{nLi} or q_{Li}. The $\dot{q}_{nL}$ and q_L can be calculated with the formulae pointing at the accessory line

$\dot{q}_{nL}$ ton ha^{-1} day^{-1}

0.18

0.500 ← $\dot{q}_{yi}$ ton ha^{-1} day^{-1}

0.300   0.200

0.16

$q_y = 0.160$

0.14

0.140

0.12

0.120

0.10

0.100

0.08

0.80

0.06

0.60

0.04

0.02

$\left(1 - \dfrac{\dot{q}_{Li}}{\dot{q}_{nLi}}\right)\left(1 - \dfrac{\dot{q}_{Li}}{\dot{q}_{yi}}\right) = F$

100 120 140 160 180 200 220 240 260 280 300 320 340

→ t days

$\dot{q}_y$ ← ton ha^{-1} day^{-1}

0.500 0.400 0.300 0.200 0.100

$\dot{q}_{Lmax.}$

0.160

0.120

0.080

0.040

t$_e$
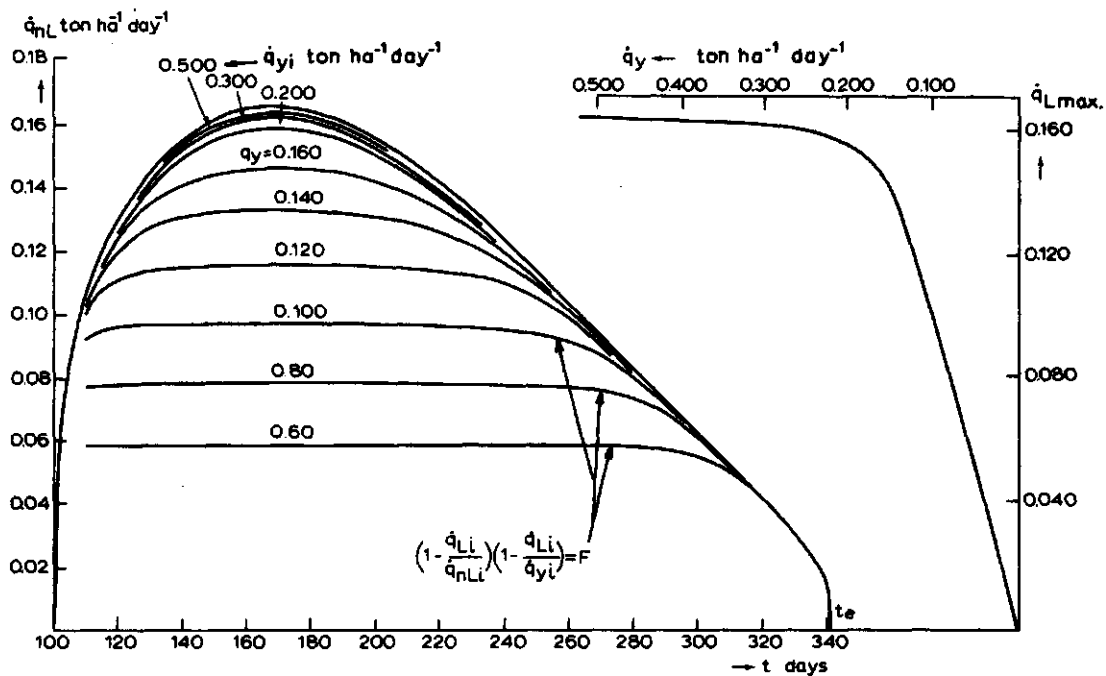
Fig. 4. By changing the limiting level of the additional growth factor to constant levels of the growth rate, differing from 60 kg day^{-1}ha^{-1} to 500 kg day^{-1}ha^{-1}, the limiting influence can be shown. In the curve given at the right hand side for the level $\dot{q}_y$ of the limiting factor versus the maximally limited growth rate for the time factor $\dot{q}_{L\ max}$ the decrease in growth rate for strong limiting effects is nearly equal to the difference between $\dot{q}_{nL}$ and $\dot{q}_y$. For limiting levels which are higher than $\dot{q}_{nL\ max}$ still a decrease in growth rate equal to the difference between $\dot{q}_{nL\ max} - \dot{q}_{L\ max}$ is found

In fig. 4, however, it is obvious that the high levels of growth rate $\dot{q}_y$ of 200 to 500 kg ha^{-1}day^{-1} still exert a lowering effect on the growth rate $\dot{q}_L$ due to the combined other factors. This forcibly leads to the conclusion that every growth factor, irrespective of its limiting level exercises a limiting influence, be it that this influence is rather small if the growth level for the additional factor $\dot{q}_y$ is higher than the level of the growth rate $\dot{q}_L$ of the combination of other factors. This effect is indicated at the right hand side of fig. 4. In this inserted graph the level of the additional factor $\dot{q}_y$ is plotted against the maximum growth rate $\dot{q}_{L\ max}$ for the combined effect of the growth factors.

It is often considered that if the fertility level for a factor is high and it will allow to produce a high yield, the effect of such a factor can be neglected. The formula states, however, that this assumption is not in accordance with a diffusion based growth equation. The experiments in which a number of factors is consciously brought to a high level to minimize their influence is for practical purposes not so very wrong. Depending on the accuracy of the experimental results the neglect of these factors can be allowed. The procedure of neglecting non-limited factors lacks, however, up to now a well defined theoretical foundation.

The equations which were used in fig. 3 and 4 are indicated in fig. 3 near the related curves for q and $\dot{q}$. These formulae can be used to determine the parameter values by applying a curve fitting technique. In this case, however, the observations of q and t, in a number equal to the number of unknowns, were used to calculate not an adjustment but a solution for the parameter values.

The temperature factor

The temperature factor is accounted for in fig. 5. The solution of $\dot{q}_{n\ L}$ and q_{nL} is in fig. 5 indicated near the related curves. It is obvious that growth is rather closely related to temperature, probably because so many growth factors are dependent on diffusion constants which depend in their turn on temperature. However, the shape of the derivative for the growth rate indicates clearly that the curve for q is not a straight line but starts and ends with a gradient $\dot{q}$ approaching zero.

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Temperature alone cannot explain the rate of growth of a plant. The maximum growth rate appears to be 8,5 kg ha^{-1}(degree days)$^{-1}$. This compares with a growth rate in fig. 3 of 166 kg ha^{-1}day^{-1}. In fig. 5 along the horizontal axis the number of days and the temperature sum are both indicated so the growth rate according both variaties can be read.

The rather close relation between temperature and the moisture flow characteristics has as a consequence that it is not certain whether the elaboration of accounting for temperature in itself corrects the time factor. Many other growth factors probably are adjested as well and at the same time as for temperature. The values of the corrections on the time variate therefore are probably more of a statistical nature than that they represent a physical relation. Investigations aiming at splitting the temperature effect into an effect on the time factor and an effect on moisture flow are therefore advisable.

Influence of an irreversible damage to growth by limiting factors

In an earlier paper (VISSER, 1969) an irreversible effect was shown of the deficiency with respect to soil moisture as growth factor. The desiccation damaged the productivity of a crop over a far longer time than the period of actual deficiency lasted. A plant can be damaged to an extent which only allows a slow repair or none at all. In fig. 6 this effect is demonstrated by means of results of a sprinkled and a non-sprinkled field during a 10-day dry period. The strongly reduced evaporation caused a decrease in growth rate which in the following period was not made up any more.

A temporary slight deficiency of an intensity as occurs frequently as result of a disbalance of evaporation and capillary rise will, dependent on the soil moisture store, cause a reduced growth rate only during the short dry spell. If the intensity of the moisture deficiency increases, the decreased growth rate will only slowly recover. This gives a lag of yield development that lasts longer than the period of temporary deficiency. In the most severe case growth will stay at the reduced rate till the end of the growth period.

$\dot{q}_{nL}$ $\left(\text{kg. ha}^{-1}(\text{degree day})^{-1}\right)$

q_{nL} ton ha^{-1}

q_{nL} (t/ha)

$q_{nLi} = 1{,}191$

$$\underset{\underset{\alpha}{\uparrow}}{\underset{\underset{q_{nLi}-0}{}}{\underset{1{,}032}{\overset{\overset{c}{\downarrow}}{}}} \overset{\overset{b}{\downarrow}}{\underset{\underset{q_o}{\uparrow}}{\frac{T_L-78{,}6}{}}} \overset{\overset{T_o}{\downarrow}\,\overset{T_e}{\downarrow}}{\underset{\underset{Q}{\uparrow}}{\frac{1}{17300-q_{Li}}}} } \cdot \frac{1}{2492{,}3-T_L}$$

$$\underset{\underset{Q}{\uparrow}}{\frac{(q_{nLi}-0)^{1{,}032}}{17300-q_{nLi}}} = \underset{\underset{d}{\uparrow}}{1{,}218} \left[\overset{\overset{T_o}{\downarrow}}{\underset{\underset{T_e}{\uparrow}}{\frac{(T_L-78{,}6)}{2492{,}3-T_L}}}\right]^{\overset{c}{\underset{1{,}191}{b}}}$$

t_o 80 100 120 140 160 180 200 220 240 $\rightarrow t$ 260 280 300 320 340 t_e

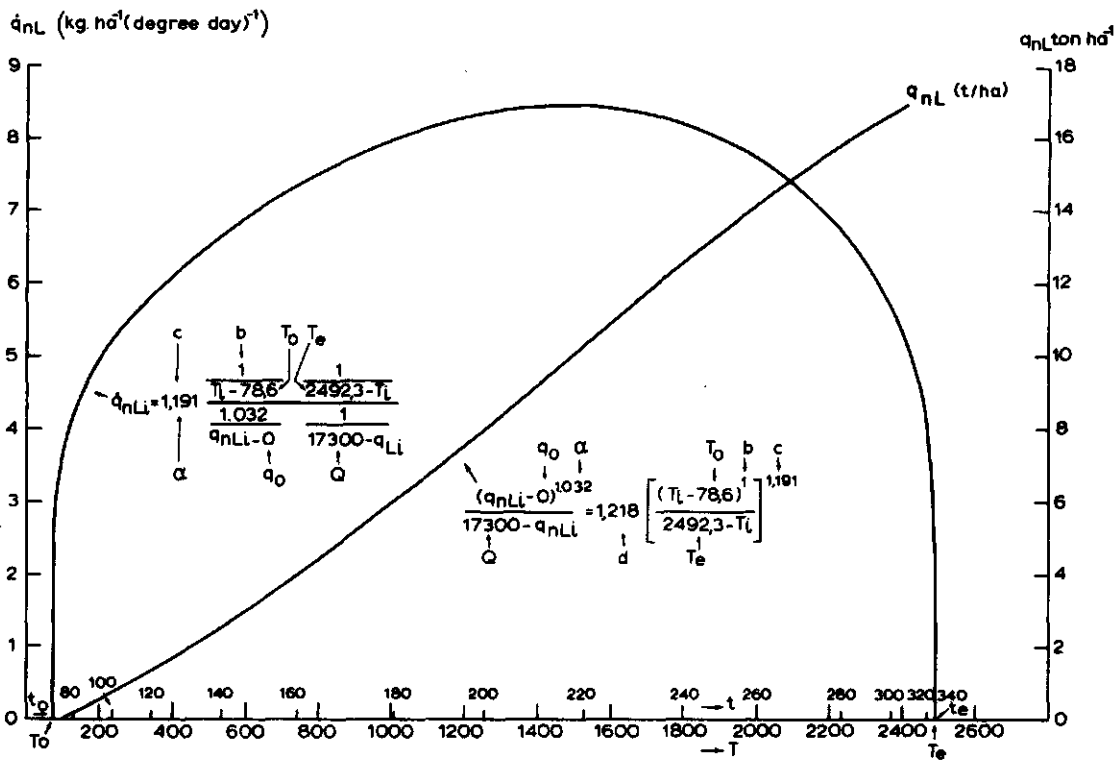T_o 200 400 600 800 1000 1200 1400 1600 1800 2000 2200 2400 2600 $\rightarrow T$ T_e

Fig. 5. The temperature influence T alone is insufficient to explain
the S-shaped yield curve q as is proved by the curved shape
of the growth rate curve. The values of a and b, however,
for this grassland example are rather near unity. The tempe-
rature has the most outspoken influence on q in the denomi-
nator, as was to be expected because the temperature sum
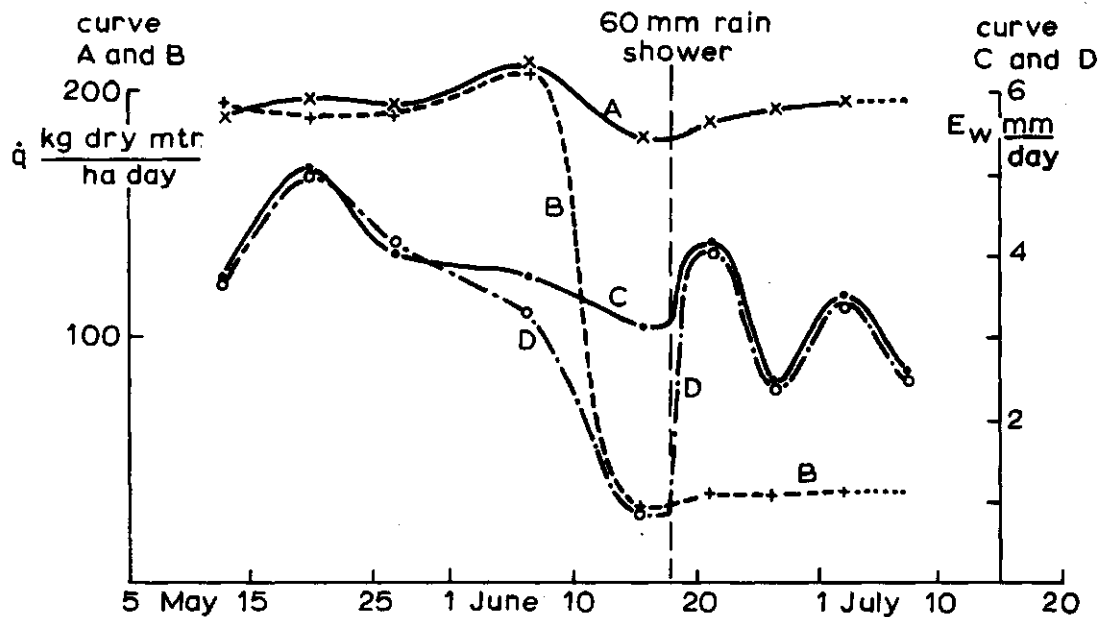resembles rather closely a yield deficit Q-q in the growth
rate equation

Fig. 6. A dry spell from June 10 to 20 decreased the growth rate
- curves A and B - as well as the evaporation - curves C
and D. The rainshower increased the evaporation on the
sprinkled field - curve C - as well as on the non-sprinkled
field - curve D. Although the evaporation of the non-sprinkled
field - curve D - ascended back to its original height, the
growth rate, because of an irreparable damage to the growth
capacity of the crop did not reach its original level again
- see curve B. The cells present at the beginning of the dry
spell are apparently damaged in such a way that the capacity
to grow largely has been lost. This influence probably affects
the value of $q-q_o$ and may make $q'_o = q_o + \Delta_2 q$ a function of
time - see equation (27)

No functional relation describing the speed of repair of the damaged production capacity of the plant is at this moment available to improve the growth equation. In fig. 3, however, it is striking that 110 deficient days reduce the yield with only 18%. Experience shows that such a relatively small damage may already be expected of a shorter sequence of deficient days.

The damage due to deficiency is in the previous pages considered to be suffered by the cells $Q-q$ still to appear and not by the already present cells $q-q_o$. If, however, the reduction in growth is not only due to the future cells failing to appear, but also to damage of the present cells reducing their cell division activity, then the reduction is a function of $(Q-\Delta_1 q)-q_o$ as well as of $q-(\Delta_2 q+q_o)$.

The equation for the cell division under influence of adverse factors then becomes:

$$\frac{dC}{dq} = \left(\frac{a}{q_i-(q_o+\Delta_2 q_i)} + \frac{1}{(Q-\Delta_1 q_i)-q_i} \right) \tag{27}$$

The value of $\Delta_1 q = Q_{i-1}-Q_i$ could be calculated. All data necessary for this purpose are available. For the $\Delta_2 q$ in the $q-q_o$ term no relation can be put forward, however, and only a statistical relation might be devised. The $\Delta_2 q$ as well as the $\Delta_1 q$ are integrated in the course of such a calculation. Further it is known that the deficiency in one factor has a far more adverse effect than the deficiency in another factor.

This relation will be of a kind in which for small values of $\Delta_1 q$ the value of $\Delta_2 q$ will be nearly zero. For large values of $\Delta_1 q$, however, the value of $\Delta_2 q$ will approach a value of such a magnitude that it will cause the value of $q-(\Delta_1 q+q_o)$ to become negative within the duration of plant life, the value of q to become imaginary and the plant to die.

As regards the effect of time the problem of adverse influences has only been touched as in this respect insufficient research has been done. As long as a deficiency is not too severe, however, this part of the productivity model probably can be neglected or extremely simplified.

Summary

The aim of a model for yield or for growth rate is to predict
what the effect is of human intervention in the total result of the
complex of productivity factors.

This complex of interacting factors was described by a general
equation, defining the process according which the plant takes up and
integrates the material supplied, as governed by growth factors which
serve the plant as nutrient or growth promoting influences. This gene-
ral function given in formula (4) is based on the law of diffusion. Next
to the general function special functions for each growth factor exist,
of which the simplest shape is a linear relation. Such a special
formula was developed for the factor time, which is weighted with
temperature. This time function is described in formula (5). In the
general function a number of special functions has to be inserted, to
describe the plant environment in as much detail as the investigation
requires. Fundamentally it would be necessary to insert all growth
factors in the growth model. They can find their already indicated
place in the formula but with more than a few factors the use of a
detailed description of the environment becomes too laborious to
solve.

The formula for the combined growth factors, time included,
is presented in formula (20). This formula can be given the shape
of formula (22) which allows the calculation of the yield $X = \dot{q}_L$ when
the growth functions according the time influence and the other ad-
ditional factors are given.

An example of the interrelation of the time factor with some
additional factor according formula (20) or (21) is given in fig. 3.

Without an additional factor the value of $Q = Q_{max}$ in formula (5)
remains constant. When, however, a limiting factor reduces the
yield, then also the Q-value decreases to $Q = Q_t$. The bell shaped
curve, indicated with $\dot{q}_{nL}$, represents the growth rate according
the special equation. The influence of the limiting factor on the
growth rate is indicated by the curve described as $\dot{q}_L$. By inte-
gration of the daily growth rates the yield curve for the non-limited
special equation is indicated with $\dot{q}_{nL}$ and the ultimate yield $Q_{nL} =$

Q_{max}. For the limited yield, calculated with the combined factors the curve is indicated with q_L and Q_L. This represents the actual yield.

In fig. 4 the curves for the limited growth rate are given for different constant intensities of the non-limited representation of the growth rate for the additional growth factor. This graph shows that also for high values of $\dot{q}_y$ still a small limitation in growth rate is present.

In fig. 5 an experiment is given of the calculation carried out for the temperature corrected time influence. It is shown that the temperature influence resembles to some extent the influence of the dry matter $Q-q$ still to be produced. But the temperature effect is not compensating the growth deficit entirely.

Consideration is given to the possible necessity not only to correct the value of Q_{max} to Q_t by subtracting a magnitude $\Delta_1 q = Q_{max} - Q_t$ but also to apply an identical correction to the lowest yield q_0 according $q_0 + \Delta_2 q = q_a$. The calculation is carried out with $q-q_a$ instead of $q-q_0$.

In fig. 6 is shown that a severe limiting influence will decrease the capacity of the already existing cells $q-q_0$ to resume dry matter production. The process of the reaction of the plant on adverse conditions is not yet sufficiently clear to be fully represented in a model of plant growth. Equation (20), however, seems to be a reliable formula to calculate the actual plant production and the yield parameters or to predict a future yield or the effect of an intervention in the growth process by nature or by man.

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