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An attempt at describing the growth of live organisms by means of a difference-differential equation

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Abstract

An attempt is made to create a formal growth model based on a difference-differential equation. The solution of this type of equation is a function of a continuous variable and of a variable assuming natural values. By using the Laplace transformation in respect to time and then solving a specific linear difference equation, a final relation showing the dependence of the amount of dry matter on a natural number and time — $w_n(t)$, was obtained. This function can be, in a certain sense, a generalization of the known Gregory-Naidenov monomolecular function. For $n = 1$ the function $w_n(t)$ transforms into a relation similar to the Mitscherlich equation, for $n > 1$, its graphs have a characteristic sigmoid shape. Numerical methods are necessary to work out specific forms of the function $w_n(t)$.

Key words: growth analysis, mathematical model, difference-differential equation

Many various mathematical functions describing the growth of living organisms can be found in biological literature (Whaley 1961, Richards 1969, Walter and Lamprecht 1976, Żelawski and Lech 1980, Żelawski 1981, France and Thornley 1984, Sztencel and Żelawski 1984). They can be purely descriptive functions (e. g. multinomials), exponential functions as solutions of certain differential equations, functions based on biological premises (Bertalanffy 1973), or generating generalized models of growth (Richards 1969, Savinov et al. 1977).

It seems that the most universal and worthy of particular attention are the generalized equations which encompass a certain group of functions depending on the value of a specific parameter. Of course, one should keep in mind that the physiological process of growth of living organisms, especially plants, is complicated, dependent on many internal and external factors. When constructing a mathematical model of growth, the high phenotypic variability of plants must be taken into account, as well as the very significant modifying influence of the environment and the fact that the final dimensions of the plant are not predetermined.

In face of the above limitations, it is hard to expect that a universal growth model based on biological premises and explaining this process in physiological terms, can be created. Nonetheless, growth curves usually have a characteristic sigmoid shape which can be described by mathematical equations. Therefore, it seems purposeful to apply certain equations to the analysis of completed growth processes, that is, when the maximal value of growth is know, e.g. the dry matter of plants.

In biological papers, the functions found most often are those obtained as the result of integration of specific differential equations. It is assumed in such cases that growth is a process continuous in time, and that its rate is proportional to certain relationships between the maximum and present value of growth.

In this study, an attempt is made to create a formal growth model based on a difference-differential equation. This type of equation describes processes in which the value being sought is at the same time a function of a continuous variable and a function of a discrete variable which assumes natural values. These types of equations are used in technical sciences, for example (Jenson and Jeffreys 1963, cit. in Traczyk and Mączyński 1970), while they are not usually found in biological literature on growth analysis of live organisms.

Assuming that the mass of an organism is a function of time t (continuous variable) and a function of a discrete variable n ($n = 1, 2, 3...$), that is, $w_n(t) = w(n, t)$ and accepting for $n = 0$ the highest final value of growth $w_0(t) = w_{max}$, then for each natural value n, a specific curve which is a function of time should be obtained. Assuming next that the growth rate is at all times proportional to the difference between the masses of the organisms differing by a factor of 1 in their value of n, a difference-differential equation of a similar type as the differential equation used in growth analysis, will be obtained.

$$\frac{dw_n(t)}{dt} = k\,[w_{n-1}(t) - w_n(t)],$$

where: w — a growth value, e.g. dry matter; t — time; k — constant ($k > 0$); $n \in N$.

The method of solving such equations depends on using the Laplace transformation on time, t, and then solving the difference equation.

$$\mathscr{L}\{w_n(t)\} = W_n(s),$$

$$sW_n - w_n(0) = k \cdot W_{n-1} - k \cdot W_n.$$

Assuming that $w_n(0) = 0$, that is at time $t = 0$ for each n, $w_n = 0$:

$$(k+s)\,W_n - k \cdot W_{n-1} = 0,$$

a linear difference equation will be obtained. If $W_n = EW_{n-1}$ (E — translation operator), then:

$$[(k+s)\,E - k]\,W_n = 0.$$

Hence the general solution has the form (Korn and Korn 1968):

$$W_n = C\left(\frac{k}{k+s}\right)^n.$$

It was taken that $w_0(t) = w_{max}$, so $W_{n=0} = \mathscr{L}\{w_0\} = \frac{w_{max}}{s}$ and $C = \frac{w_{max}}{s}$.

The final solution of the linear difference equation is as follows:

$$W_n = \frac{w_{max}}{s}\left(\frac{k}{k+s}\right)^n.$$

In turn, the original w_n transform W_n should be found:

$$w_n(t) = \mathscr{L}^{-1}\{W_n(s)\}.$$

By application of the convolution theorem and use of the Laplace transformation tables (Korn and Korn 1968) the following is obtained:

$$w_n(t) = w_{max} \cdot k^n \cdot \mathscr{L}^{-1}\left\{\frac{1}{s}\right\} \cdot \mathscr{L}^{-1}\left\{\frac{1}{(k+s)^n}\right\},$$

$$w_n(t) = w_{max} \cdot k^n \cdot \int_0^t \frac{\tau^{n-1} \cdot e^{-k\tau}}{(n-1)!}\,d\tau.$$

The integral given above can be calculated by integrating by parts n times:

$$\int_0^t \frac{\tau^{n-1} \cdot e^{-k\tau}}{n-1!}\,d\tau = -\frac{t^{n-1} \cdot e^{-kt}}{k\,(n-1)!} - \frac{t^{n-2} \cdot e^{-kt}}{k^2\,(n-2)!} - \dots - \frac{e^{-kt}}{k^n} + \frac{1}{k^n}.$$

Finally, the relationship $w_n(t)$ is obtained:

$$w_n(t) = w_{max}\left\{1 - e^{-kt} - \frac{(kt)^1}{1!}e^{-kt} - \dots - \frac{(kt)^{n-1}}{(n-1)!}e^{-kt}\right\},$$

$$w_n(t) = w_{max}\left\{1 - \left[1 + \frac{(kt)^1}{1!} + \dots + \frac{(kt)^{n-1}}{(n-1)!}\right]e^{-kt}\right\},$$

$$w_n(t) = w_{max}\left\{1 - \left[\sum_1^n \frac{(kt)^{n-1}}{(n-1)!}\right]\cdot e^{-kt}\right\}.$$

The function $w_n(t)$ given above can be, in a certain sense, a generalization of the Gregory-Naidenov monomolecular function (Richards 1969,

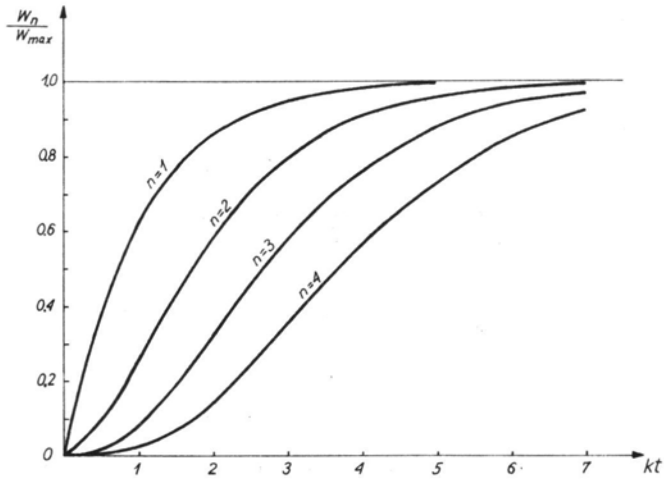

Fig. 1. A graph of the relation $w_n/w_{max} = f(n, kt)$

Żelawski and Lech 1980): $w(t) = w_{max}(1 - b \cdot e^{-kt})$, where b has been substituted by the power series with elements dependent on the natural number n.

It can be shown that the series $\sum_1^n \frac{(kt)^{n-1}}{(n-1)!}$ is convergent for each t and that its sum for $n \to \infty$ equals e^{kt}.

The function $w_n(t)$ has its inflexion point at

$$t^* = \frac{n-1}{k}.$$

For $n = 1$, the function $w_n(t)$ does not have an inflexion point; a relationship similar to the Mitscherlich equation is obtained then (Ware et al. 1982, Sztencel and Żelawski 1984):

$$w(t) = w_{max}(1 - e^{-kt}).$$

The absolute growth rate (GR) $dw_n(t)/dt$ for any natural number n equals:

$$\frac{dw_n(t)}{dt} = k \cdot w_{max} \cdot e^{-kt} \cdot \frac{(kt)^{n-1}}{(n-1)!}.$$

In this way, by solving a specific difference-differential equation, a family of functions is obtained, whose graphs can be useful in describing the growth processes of living organisms.

On Fig. 1 the relationship:

$$\frac{w_n}{w_{max}} = f(n, kt),$$

is presented for the first four natural numbers; Fig. 2 presents the graph of the relation

$$\frac{dw_n/dt}{k \cdot w_{max}} = f(n, kt).$$

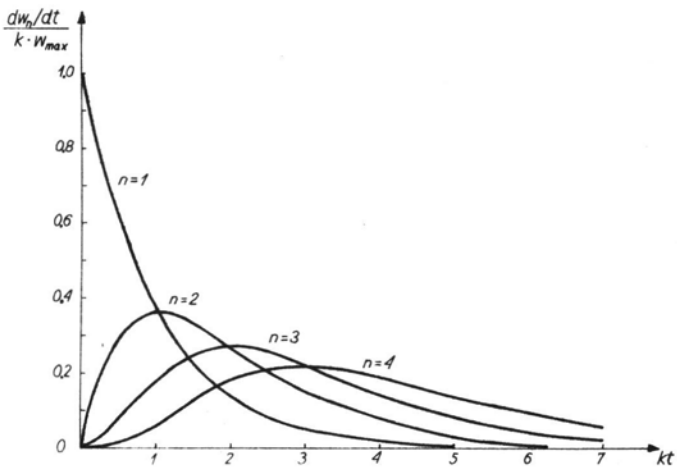

Fig. 2. A graph of the relation $\frac{dw_n/dt}{k \cdot w_{max}} = f(n, kt)$

Due to the rather complicated of the generalized growth function, it is necessary to use numerical methods in order to determine the specific values of parameters k and n.

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Próba opisu wzrostu żywych organizmów za pomocą równania różnicowo-różniczkowego

Streszczenie

W pracy podjęto próbę stworzenia formalnego modelu wzrostu opartego na równaniu różnicowo-różniczkowym. Rozwiązaniem równania różnicowo-różniczkowego jest funkcja zmiennej ciągłej oraz zmiennej przyjmującej wartości naturalne. Stosując przekształcenie Laplace'a względem czasu, a następnie rozwiązując konkretne liniowe równanie różnicowe, uzyskano ostateczną zależność wielkości suchej masy od liczby naturalnej i czasu — $w_n(t)$. Otrzymana funkcja może być w pewnym sensie uogólnieniem znanej funkcji monomolekularnej Gregory'ego-Naidenova. Dla $n = 1$ funkcja $w_n(t)$ przechodzi w zależność podobną do równania Mitscherlicha, a dla $n > 1$ jej wykresy mają charakterystyczny sigmoidalny kształt. Do wyznaczania konkretnych postaci funkcji $w_n(t)$ niezbędne jest stosowanie metod numerycznych.