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MATHEMATICAL MODEL FOR THE PHYSIOLOGICAL
CLOCK AND GROWTH

*FYSIOLOGISEN KELLON JA KASVUN MATEMAAT-
TINEN MALLI*

Jukka Sarvas



SUOMEN METSÄTIETEELLINEN SEURA

Suomen Metsätieteellisen Seuran julkaisusarjat

ACTA FORESTALIA FENNICA. Sisältää etupäässä Suomen metsätaloutta ja sen perusteita käsitteleviä tieteellisiä tutkimuksia. Ilmestyy epäsäännöllisin väliajoin niteinä, joista kukin käsittää yhden tutkimuksen.

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PREFACE

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Helsinki, June 4, 1976

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Hämeenlinna 1977, Arvi A. Karisto Osakeyhtiön kirjapaino

1. INTRODUCTION AND PREFACE OF THE MAIN RESULTS

The present investigation is based partly on the author's reports to the Finnish Forest Research Institute, entitled »Theory of the physiological clock» (1970) and »Homogeneous process and physiological clock» (1972), both unpublished.

My interest in the present subject was aroused when I became acquainted with the investigations conducted by the late Professor Risto Sarvas, concerning the annual cycle

of development of forest trees. Many of the principal ideas, developed in the above reports and in the present investigation stem from frequent discussions with Professor Sarvas, regarding this subject. I am very grateful to him.

The Finnish language manuscript was translated into English by Mrs. Marja Dethlefsen, to whom I tender my thanks.

Helsinki, June 4, 1976

JUKKA SARVAS

In the present paper, the concept of a physiological clock and its function in biological processes is studied in strictly mathematical terms. The starting point is the heat sum method employed by Risto Sarvas (1972 and 1974). In the form introduced by him a heat sum is an integral expression whose formula is determined experimentally from the object of research. The function of this heat sum as a physiological clock can be explained mathematically and so satisfactorily that there is no need for intuitive a priori assumptions which are often unavoidably associated with different heat sums and the concept of a physiological clock. Furthermore, his approach to the physiological clock provides a conceptually clear model and by following it we can define the physiological clock in fairly general terms.

J. 2. R. Sarvas applied the heat sum method in studying the annual cycle of development of forest trees. This is a biological process which does not initially involve any measurable quantity or numerical scale but consists of a chain of successive events called cardinal phases. They include e.g. the different phases of meiosis, anthesis, syngamy and the autumn and winter dormancies.

In the first part of this paper (Chapters 1-3) we shall consider a general process of this kind and define a physiological clock for it. Moreover, we wish to study how the formula pertaining to this clock can be derived and its components calculated from observational data.

We assume that the progress of the

process, which we call the physiological age of the process, has been determined. After this we shall define the physiological clock of the process (see Definition 1.1). This will be, roughly speaking, a mathematical formula from which it is possible to compute the cardinal phase in which the process is at a given time t (in other words: the physiological age of this cardinal phase is computed), provided that the environmental factors and their dependence on time during the process are known.

Furthermore, we shall so define the physiological clock that it meets the following natural normalization condition: if, during the entire process, the environmental conditions remain in the same (definitely fixed) basic state, the time measured by the physiological clock coincides with ordinary time. From this normalization condition it follows that the physiological clock has been rendered unique as will be shown below (see Chapter 2.5).

Now that the concept of the physiological clock of the process has been given a precise form, the next step is to derive its explicit mathematical formula and present methods by which the components of this formula can be calculated from the experimental data obtained from the process in question. Generally speaking, this task can be very difficult. However, if the process meets some condition that sufficiently simplifies the situation, the formula of its physiological clock can be derived. A condition of this kind was used by R. Sarvas (1972) and here we call it the *homogeneity condition*. The validity of this condition can be checked (at least in principle) by simple experiments regarding the process in question.

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1. INTRODUCTION AND SUMMARY OF THE MAIN RESULTS

1.1. In order to facilitate description of biological developmental and growth processes, the concept of a physiological clock is often resorted to. The progress of the process is then thought of as depending on a physiological clock that is specific to this process and the running of which might differ considerably from that of an ordinary clock. Especially, different heat sum methods have frequently been employed as physiological clocks.

In the present paper, the concept of a physiological clock and its function in biological processes is studied in strictly mathematical terms. The starting point is the heat sum method employed by Risto SARVAS (1972 and 1974). In the form introduced by him a heat sum is an integral expression whose formula is determined experimentally from the object of research. The function of this heat sum as a physiological clock can be explained mathematically and so satisfactorily that there is no need for intuitive a priori assumptions which are often unavoidably associated with different heat sums and the concept of a physiological clock. Furthermore, his approach to the physiological clock provides a conceptually clear model and by following it we can define the physiological clock in fairly general terms.

1.2. R. SARVAS applied the heat sum method in studying the annual cycle of development of forest trees. This is a biological process which does not initially involve any measurable quantity or numerical scale but consists of a chain of successive events called cardinal phases. They include e.g. the different phases of meiosis, anthesis, syngamy and the autumn and winter dormancies.

In the first part of this paper (Chapters 1–3) we shall consider a general process of this kind and define a physiological clock for it. Moreover, we wish to study how the formula pertaining to this clock can be derived and its components calculated from observational data.

We assume that the progress of the

process depends on time and environmental factors. The environmental factors involved may include e.g. heat, light, moisture etc. In order to be able to observe the progress of the process we shall pick out from it easily distinguishable successive events which we call *cardinal phases*. Each cardinal phase is assigned, in a manner that will be described in detail later, a numerical value which we call the *physiological age* of the cardinal phase concerned. After this we shall define the physiological clock of the process (see Definition 2.2 on page 7). This will be, roughly speaking, a mathematical formula from which it is possible to compute the cardinal phase in which the process is at a given time t (in other words: the physiological age of this cardinal phase is computed), provided that the environmental factors and their dependence on time during the process are known.

Furthermore, we shall so define the physiological clock that it meets the following natural normalization condition: if, during the entire process, the environmental conditions remain in the same (beforehand fixed) basic state, the time measured by the physiological clock coincides with ordinary time. From this normalization condition it follows that the physiological clock has been rendered unique as will be shown below (see Chapter 2.5).

Now that the concept of the physiological clock of the process has been given a precise form, the next step is to derive its explicit mathematical formula and present methods by which the components of this formula can be calculated from the experimental data obtained from the process in question. Generally speaking, this task can be very difficult. However, if the process meets some condition that sufficiently simplifies the situation, the formula of its physiological clock can be derived. A condition of this kind was used by R. SARVAS (1972) and here we call it the *homogeneity condition*. The validity of this condition can be checked (at least in principle) by simple experiments regarding the process in question.

As the main result pertaining to our generalized physiological clock, the following emerges: if the process satisfies the homogeneity condition, then the formula of its physiological clock can be derived, and it takes the same general form as the heat sum formula presented by R. SARVAS (1972).

Particularly, in the case of the heat sum this result indicates that if temperature along with time is the only environmental factor influencing the progress of the process and the process is homogeneous (i.e. meets the homogeneity condition), the formula of its physiological clock is exactly the integral formula used by R. SARVAS (1972), and the heat sum satisfying the normalization condition mentioned above cannot be computed in any other way.

1.3. In the latter part of this paper we shall deal with growth processes. In general, by a growth process we mean a process which initially involves a measurable quantity V that grows with time and whose value $V(t)$ at time t fully indicates the phase of the process. The function $V = V(t)$ we call the *growth function* of the process. The progress of a growth process is mastered, if the dependence of the function V on time and environmental factors is known, so that the value of V can be computed whenever the environmental factors and their dependence on time during the process are known. For instance, the height growth of a tree is a growth process if we set $V(t) =$ the height of the tree at time t .

In investigating the progress of a growth process it is often assumed that the rate of growth $\frac{dV}{dt}$ depends, in addition to environmental factors, on a hypothetical quantity called the «inner state of the plant» or «physiological state of development» or «physiological age» (cf. e.g. HARI et al. 1970 and 1974, and POHJONEN 1975). Usually, the «physiological age» is then given as a mathematical expression depending on time and environmental factors.

However, the concept of «physiological age» or the form of its mathematical expression is then introduced as a somewhat arbitrary a priori assumption which is not meant to be derived, for instance, from another simpler and testable assumption.

We wish to study more closely the role of the «physiological age» in the growth process. In particular, we wish to know whether the «physiological age» that has been assigned to the physiological clock introduced above can be used in this connection. In dealing with the growth process our aim is to pursue a program similar to that employed by R. SARVAS (1972 and 1974) in investigations concerned with the construction of a mathematical model (the heat sum) for a biological phenomenon. This program consists of experimental testing of the mathematical basic assumptions, the derivation of the solution of the model exclusively from these basic assumptions, and the calculation of all unknown components of the solution directly from the experimental data obtained from the growth process itself. In this spirit we shall present two growth models, i.e. the mathematical model of a homogeneous growth process and that of a semihomogeneous one. Furthermore, we shall show that some earlier growth models (POHJONEN 1975 and HARI et al. 1970, 1974) can be reduced to these two basic types.

Especially, in the case of the homogeneous growth process, it is not necessary for the concept of «physiological age» to be included among the basic assumptions to be made regarding the model. However, in the formula of the growth function in either model appears an integral expression which, with good reason, may be called the «physiological clock» and the values of the expression the «physiological age». Furthermore, this expression coincides exactly with the physiological clock introduced earlier, provided that the growth process is first in a proper way interpreted to be a general process with cardinal phases.

2. DEFINITION OF THE PHYSIOLOGICAL CLOCK

2.1. We consider a general process P whose progress we can observe by means of its cardinal phases. We suppose that P always starts at time $t = 0$. Let x_1, \dots, x_n be the environmental factors which affect the progress of P . Environmental factors of this kind may include temperature, moisture, light, etc. We call every n -tuple (x_1, \dots, x_n) of the environmental factors a *state of the environment*. Mathematically, a state of the environment is thus a vector in the n -dimensional (euclidean) space R^n .

Those states of the environment in which P does not progress at all we call *static* and the others non-static. We single out one of the non-static environmental states (a_1, \dots, a_n) and call it the *basic state of the environment* (with regard to P).

When the state of the environment changes, every environmental factor x_i , $i = 1, 2, \dots, n$, is a function of time t or $x_i = x_i(t)$, $t \geq 0$. Let the n -tuple of these functions be the function

$$E = E(t) = (x_1(t), x_2(t), \dots, x_n(t)),$$

which at any time $t \geq 0$ fully describes the state of the environment (in relation to P). Mathematically, E is thus a function from the set of non-negative real numbers to the space R^n or $E: [0, \infty) \rightarrow R^n$. We call a function like this an *environmental function*. We assume that environmental functions are at least piecewise continuous. The constant function corresponding to the basic environmental state (a_1, \dots, a_n) is denoted by E_0 , i.e. $E_0(t) = (a_1, \dots, a_n)$ for all $t \geq 0$.

Concerning the cardinal phases of P we assume the following. Having once started, the process is, at every moment, in some cardinal phase. If the environment is in the basic state (a_1, \dots, a_n) all the time, the process passes through all of its cardinal phases in such a way that it at different moments is in different cardinal phases (before the end of the process). The part between two successive cardinal phases, M_1 and M_2 , of the process P is called a *cardinal interval* $[M_1, M_2]$.

We now assign every cardinal phase M its physiological age $s(M)$ as follows:

2.2. DEFINITION. The *physiological age* $s(M)$ of an arbitrary cardinal phase M of the process P is the time which P requires to progress from its initial phase to the phase M , provided the environment is in the basic state (a_1, \dots, a_n) all the time.

2.3. By the physiological clock C of the process P we mean, roughly speaking, a mathematical formula from which we can compute the cardinal phase M in which P is at time t (or, more precisely, we compute the age $s(M)$), provided we know that the environmental changes have occurred according to the function E . We set the definition:

2.4. DEFINITION. The *physiological clock* $C = C(t, E)$ of the process P is a function depending on time t and on the environmental function E and is defined by the following equation: for any E and any $t \geq 0$

$$C(t, E) = s(M_t),$$

where M_t is the cardinal phase in which P is at time t , when the environment changes according to the function E during the process.

2.5. From the definition of the physiological clock it immediately follows that if the environment is in its basic state all the time, the time indicated by the physiological clock coincides with ordinary time, that is,

$$(2.6) \quad C(t, E_0) = t \text{ for all } t \geq 0.$$

This natural normalization condition implies an important uniqueness property of the physiological clock. Let P_1 and P_2 be two different processes (the cardinal phases of which might be entirely different events). We say that P_1 and P_2 are synchronized if each cardinal phase M_1 of P_1 is matched by some cardinal phase M_2 of P_2 in such a way that M_1 and M_2 always occur simultaneously regardless of changes

in the state of the environment, provided that the processes occur in the same environment and start simultaneously. We now prove:

2.7. THEOREM. If P_1 and P_2 are synchronized processes, it follows that their physiological clocks C_1 and C_2 are identical, i.e. $C_1 = C_2$.

PROOF. Let E be an arbitrary environmental function and $t > 0$. We must show: $C_1(t, E) = C_2(t, E)$. Let M_1 be the cardinal phase of P_1 in which P_1 is at time t when the environment has complied with function E . Then $s(M_1) = C_1(t, E)$ holds for the physiological age $s(M_1)$ of M_1 . Since the processes P_1 and P_2 are synchronized, M_1 is matched by some cardinal phase M_2 of P_2 in such a way that M_1 and M_2 always occur simultaneously. Hence, they also occur simultaneously when the environment remains in the basic state, i.e. $s(M_1) = s(M_2)$. Furthermore, their occurrence is simultaneous when the environment complies with function E and, therefore, at time t , process P_2 must be in the cardinal phase M_2 . Then $C_2(t, E) = s(M_2)$. Thus $C_1(t, E) = s(M_1) = s(M_2) = C_2(t, E)$. We have proved that $C_1 = C_2$. Q.E.D.

2.8. The above theorem shows that if the aim is to define the concept of a physiological clock in such a way that the physiological clock is 'synchronized' with the process (regardless of changes in the state of the environment) and, in addition, that the «clock» is to meet the natural normalization condition (2.6), there is no choice: the definition stated in (2.4) is the only possible one.

2.9. We can say that we master the progress of P if we know the formula of its physiological clock C . Before we begin to

consider different possibilities to derive this formula, one more assumption regarding the process P is necessary. In order to be able to handle the physiological clock of P within the framework of an appropriate mathematical formalism, we assume that P satisfies the following regularity condition: if an arbitrary environmental function E is approximated by a piecewise constant environmental function E_m , then at any time $t > 0$ the cardinal phase of P is, if the environment complies with E , approximately the same as when it complies with E_m or, in brief, $C(t, E) \approx C(t, E_m)$. Furthermore, this approximation is the better the more closely E_m approximates E . We formulate this condition precisely as follows: Let E be an arbitrary environmental function, $t > 0$ and let $m \geq 1$ be an integer. We subdivide the interval $[0, t]$ with points $k_0 = 0 < k_1 < k_2 < \dots < k_m = t$ into m equal subintervals, whence $k_i = i \frac{t}{m}$, $i = 0, 1, \dots, m$. We now define the function E_m by setting

$$(2.10) \quad E_m(r) = \begin{cases} E(k_{i-1}) & \text{if } k_{i-1} \leq r < k_i, \\ & i = 1, 2, \dots, m, \\ E(t) & \text{if } r \geq t. \end{cases}$$

We call E_m the m -approximation of E in the interval $[0, t]$ for $m = 1, 2, \dots$. Now we assume:

2.11. REGULARITY ASSUMPTION. If E is an environmental function and $t > 0$, then $\lim_{m \rightarrow \infty} C(t, E_m) = C(t, E)$.

As far as we can see, the above regularity assumption does not (essentially) restrict the biological behavior of the process, and that is why we do not, for instance, require experimental testing of the condition.

3. PHYSIOLOGICAL CLOCK OF A HOMOGENEOUS PROCESS

3.1. In a general case, the derivation of the formula of the physiological clock of a process can be an exceedingly difficult task. However, if the process satisfies some additional condition that sufficiently simplifies the situation, the task might turn out to be easy. However, it is always necessary to test experimentally whether or not the process really satisfies this condition. If the condition is valid, the physiological clock of the process complies with the formula derived by making use of this condition. A simplifying condition like this was introduced by R. SARVAS (1972) and in this paper we call it the *homogeneity condition*.

Consider a process P. Let $[M_1, M_2]$ be a cardinal interval of P and (x_1, \dots, x_n) a non-static state of the environment. We suppose that at time t_1 the process P is in a cardinal phase M_1 and at time $t_2 > t_1$ in a cardinal phase M_2 . Furthermore, let the state of the environment in the time interval between t_1 and t_2 remain constant (x_1, \dots, x_n) . We write

$$(3.2) \quad h(x_1, \dots, x_n) = \frac{s(M_2) - s(M_1)}{t_2 - t_1},$$

where according to the definition (2.2) of the physiological age, $s(M_2) - s(M_1)$ is the time required for the process P to progress from M_1 to M_2 when the environment remains in the basic state (a_1, \dots, a_n) . We now define:

3.3. DEFINITION. Process P satisfies the *homogeneity condition*, i.e. is *homogeneous*, if for every non-static state (x_1, \dots, x_n) of the environment and for every cardinal interval $[M_1, M_2]$ of P the ratio $h(x_1, \dots, x_n)$ depends only on the state (x_1, \dots, x_n) and not on $[M_1, M_2]$ or on the states of the environment before M_1 has been reached.

3.4. Thus, if the process is homogeneous, the ratio $h(x_1, \dots, x_n)$ is well-defined for all non-static states of the environment. We set $h(x_1, \dots, x_n) = 0$ if (x_1, \dots, x_n) is a static state. Then h is a real valued function defined for all states of the environment

and we call it the *homogeneity function* of the process P. According to formula (3.2) $h(x_1, \dots, x_n)$ is the ratio of the 'rates of development' of the process in the constant states (a_1, \dots, a_n) and (x_1, \dots, x_n) . Without restricting the biological behavior of the process, we obviously can assume that h is a continuous function.

3.5. Next will be presented the principal result pertaining to the physiological clock: if a process is homogeneous, the formula of its physiological clock can be derived and it always takes the following simple form:

3.6. THEOREM. Let P be a homogeneous process and h its homogeneity function. The physiological clock $C = C(t, E)$ of P takes the form

$$(3.7) \quad C(t, E) = \int_0^t h(E(t)) dt.$$

PROOF. Let E be an environmental function and $t > 0$. For every integer $m \geq 1$ let E_m be the m-approximation of E in the interval $[0, t]$ defined by (2.10). Since h is continuous and E at least piecewise continuous, the composite function $h(E(t))$ is Riemann-integrable and we get

$$(3.8) \quad \int_0^t h(E(t)) dt = \lim_{m \rightarrow \infty} \sum_{i=1}^m h(E(k_{i-1})) (k_i - k_{i-1}),$$

where $k_i = i \frac{t}{m}$, $i = 0, 1, 2, \dots, m$ for all $m = 1, 2, \dots$

On the other hand,

$$(3.9) \quad C(t, E_m) = \sum_{i=1}^m \left(C(k_i, E_m) - C(k_{i-1}, E_m) \right) = \sum_{i=1}^m h(E(k_{i-1})) (k_i - k_{i-1}),$$

for by the definition of the homogeneity function

$$h(E(k_{i-1})) = \frac{C(k_i, E_m) - C(k_{i-1}, E_m)}{k_i - k_{i-1}}$$

for each $i = 1, 2, \dots, m$. Thus the assertion (3.7) follows from (3.8) and (3.9) by the regularity assumption (2.11). Q.E.D.

3.10. It immediately follows from Theorem 3.6 that if two homogeneous processes have the same homogeneity function, then their physiological clocks are identical. It is to be noted that outwardly the processes can be very different, i.e. their cardinal phases can be completely different, and yet they have identical homogeneity functions. Thus, two outwardly different processes can have a common physiological clock (cf. different tree species, Section 3.14).

3.11. REMARK. Let E be an arbitrary environmental function and write $C_E(t) = C(t, E)$ for $t \geq 0$. By differentiating equation (3.7) with respect to time t we obtain

$$(3.12) \quad \frac{d}{dt} C_E(t) = h(E(t))$$

(with the possible exception of finitely many t). On the other hand, it is not difficult to show that if there is a continuous non-negative function $h: \mathbb{R}^n \rightarrow \mathbb{R}$ (\mathbb{R} = the set of real numbers) corresponding to the physiological clock C of the process P in such a way that (3.12) holds for every environmental function E (with the possible exception of finitely many t), then P also satisfies (2.11) and the homogeneity condition (3.2). We thus see that the regularity condition (2.11) and the homogeneity condition (3.2) together are equivalent to the mathematically simpler condition (3.12). Because formula (3.7) almost trivially follows from (3.12), condition (3.12) would be a clearly simpler definition of homogeneity than are (2.11) and (3.2) together. However, experimental interpretation of condition (3.12) is difficult and would obviously lead to a review of criteria similar to (2.11) and (3.12). That is why we have based our theory of the physiological clock of a homogeneous process on conditions (2.11) and (3.2) which are experimentally more adequate.

3.13. TESTING OF HOMOGENEITY AND COMPUTATION OF THE HOMOGENEITY FUNCTION FROM EXPERI-

MENTAL DATA. Experimental testing of the homogeneity of a process is simple (at least in principle) directly by definition 3.3, provided that plenty of reliable observational data are available from different cardinal intervals of the process in different constant states of the environment. If the process proves to be homogeneous, its homogeneity function is determined at the same time in accordance with equation (3.2). In practice, however, great difficulty can be encountered in carrying out the test. For instance, only a limited number of cardinal phases suitable for observation might be available. However, if the validity of equation (3.2) can be ascertained in respect of a sufficient number of cardinal phases and environmental states, the homogeneity will be largely tested and the homogeneity function approximately determined. In that case, formula (3.7) can be expected to give a satisfactory approximation for the physiological clock of the process.

The homogeneity condition in itself is a rather strict restriction for a general process and obviously there exist numerous non-homogeneous processes as well. However, if a non-homogeneous process can be divided into finitely many successive roughly homogeneous subprocesses, formula (3.7) can again be used to approximate 'piecewisely' the physiological clock of the process.

3.14. COMPARISON WITH THE PHYSIOLOGICAL CLOCK USED BY R. SARVAS IN HIS INVESTIGATIONS IN 1972 AND 1974. The theory of the physiological clock presented above is a generalization of the physiological clock used by R. SARVAS in his investigations made in 1972 and 1974 (i.e. his heat sum method). He applied the method to the study of the annual cycle of development of forest trees.

The process he considered was the annual cycle of development of an individual tree. There is only one essential environmental factor that influences the progress of the process, i.e. temperature T , and so the environmental function $E(t)$ takes the form $E(t) = T(t)$ for $t \geq 0$. The cardinal phases used for the observation of the process included the different phases of meiosis,

opening of the male catkins, anthesis, syngamy, autumn dormancy (dormancy I) and winter dormancy (dormancy II).

The annual cycle of development is not, in its entirety, a homogeneous process but is divided into three homogeneous parts: winter dormancy, the active period, and autumn dormancy. For every subprocess an appropriate temperature has been chosen as the basic state of the environment: for the winter dormancy this temperature is 2° C, for the active period 2° C (or 2.15° C, to be exact) and for the autumn dormancy 3.5° C. The homogeneity function of each subprocess has been determined experimentally. On the basis of the experimental results it has been possible to assume that in each subprocess the homogeneity function is the same for all the investigated tree species and even for the respective individual trees. Thus, in each subprocess, there is only one physiological clock and it is common to all the individual trees of the investigated tree species.

The homogeneity function of the active

period was called «the rate of progress of the active period» by R. SARVAS. The homogeneity functions of autumn and winter dormancies were named analogously. The active period provides numerous appropriate cardinal phases for the arrangement of tests and the results obtained support the opinion that this subprocess is homogeneous. In the case of autumn and winter dormancies, the number of appropriate cardinal phases available have not been sufficient for the testing of homogeneity. However, the results obtained do not occasion the abandonment of the opinion that these subprocesses, too, are homogeneous (within the limits of satisfactory accuracy). Furthermore, it has been possible by experimentation to determine fairly accurately the corresponding homogeneity functions for all the three subprocesses. Their graphs were presented by R. SARVAS in his 1974 paper (Fig. 22, page 95; for the figure, the functions have been so normalized that each function assumes the value 1 at temperature T = 3.5° C).

4. GROWTH PROCESS AND GROWTH FUNCTION

4.1. We consider a growth process P whose growth function is $V = V(t)$. The function $V(t)$ is then a function of time and of the state of the environment. When necessary, we express this by writing $V(t) = V_E(t)$ where E is the environmental function which determines the state of the environment during the process. We assume that the function $V = V_E(t)$ is continuously differentiable with respect to time t for all environmental functions E .

The *rate of growth* is defined as $\frac{dV}{dt} = V'(t) = V'_E(t)$, or, in other words, as the derivative of the growth function with respect to time. We further assume that $V_E(0) = 0$ for all environmental functions E , which assumption only refers to an appropriate choice of the zero point of the growth scale.

We often consider the behavior of the growth function when the environment remains in some constant state $z = (x_1, \dots, x_n)$. The growth function corresponding to this constant state is denoted by $V_z(t)$, i.e.

$V_z(t) = V_E(t)$, $t \geq 0$, where $E(t) = z$ for all $t \geq 0$.

The graph of the function $V_z(t)$, drawn on the xy -plane, is called a *growth curve* (corresponding to the constant state z) and denoted by $y = V_z(x)$, as usual.

We further suppose that $V'_{z_0}(t) > 0$ for all $t \geq 0$ where $V_{z_0}(t)$ is the growth function corresponding to the basic state $z_0 = (a_1, \dots, a_n)$ of the environment. In other words, we suppose that a growth process keeps proceeding without stopping if the environment constantly remains in the basic state (until the possible final end of the process).

Often a growth process is studied as a function of time in different constant states of the environment, that is, the growth curves $y = V_z(x)$ are the only concern. Or, alternatively, time is kept constant and the state of the environment is allowed to vary, i.e. we study how in a constant growing time, growth depends on different constant states of the environment. For example, Lyr et al. 1967, pages 379–395,

have studied the growth of a tree in both of the above ways. A growth model derived from inspections of this kind is often called static.

Obviously, in natural conditions the state of the environment can vary during the growth process and thus growth actually is a function of time and of the state of the environment so that both factors may vary simultaneously. In the present paper we wish to study this general case. A growth model that takes into consideration the variation in the environment during the process is often called dynamic (cf. HARI et al. 1970, 1974 and POHJONEN 1975). However, it is to be noted that in those dynamic growth models which we shall present, the 'static' growth curves play an important part: they provide the observational data from which we are to calculate the unknown components of the formula of the 'dynamic' growth function.

4.2. It is appropriate to consider a growth process as a first order differential equation and state on which factors the rate of growth $V'(t)$ depends and in what way. In a general case it can be very hard to form the differential equation required. However, if the process under consideration meets some conditions which sufficiently simplify the situation, it will be possible to form and solve its differential equation and thus derive the formula of the growth function itself.

In Chapters 5 and 6 we shall present two conditions of this kind: the *homogeneity condition* (for a growth process) and the *semihomogeneity condition* and also the mathematical models of the growth processes corresponding to these conditions.

In this paper, the mathematical model of the growth process refers to a whole which comprises the simplifying assumptions concerning the growth process or its growth function, the formula of the growth function, and the methods by which the unknown components of the formula are calculated from experimental data.

4.3. CONSTRUCTION OF A MATHEMATICAL MODEL FOR A GROWTH PROCESS. Several kinds of mathematical

models can be constructed for the same growth process, depending on the starting point or on the goal to be achieved. Consequently, we first wish to describe the program we shall follow in approaching the problem. It covers the following points:

(I) *The basic assumptions pertaining to the model.* All the assumptions made on the model should be clearly stated. The mathematical treatment of the model and, above all, the derivation of the formula of the growth function may be based exclusively on these basic assumptions (possibly excepting mathematical regularity assumptions that do not restrict the biological behavior).

(II) *Experimental testing of the basic assumptions.* The statement of the basic assumptions made on the model should be followed by a demonstration of how they can be tested experimentally (at least in principle) in the case of the growth process involved. If the growth process satisfies (exactly) the conditions of the assumptions, the growth is in (accurate) agreement with the model.

(III) *Solving the growth function and computing the components of its formula from experimental data.* The formula of the growth function is to be derived exclusively from the basic assumptions. The resulting formula often includes unknown constants or functions and it should be stated how they can be computed from experimental data. At the same time it will become evident which kinds of observational data are to be collected for the final computation of the formula of the growth function.

Often, the mathematical side of the above program is rather easy to accomplish but the experimental side can cause insurmountable obstacles. For instance, the testing of the basic assumptions can be very hard and laborious. Furthermore, it can prove difficult to collect for point (III) a satisfactory number of observational data that are accurate enough. However, if these difficulties can be overcome, the entire growth model will stand on a very firm experimental and theoretical basis.

4.4. In the spirit of the above program we shall present two growth models, i.e. the mathematical models of a homogeneous

and a semihomogeneous growth process. We shall also show that some earlier mathematical growth models (HARI et al. 1970, 1974 and POHJONEN 1975) can be reduced to these two basic types.

Often, in constructing growth models it has been found useful to employ an auxiliary quantity called the «state of development» or the «physiological age» etc. (e.g. HARI et al. 1970 and 1974). This auxiliary quantity has been introduced into the model as a kind of a priori assumption. This was considered necessary for purely biological (but weighty) reasons. Now the question arises: what is the role of an auxiliary quantity of this kind in a homogeneous and a semihomogeneous growth process.

We shall see that in the case of a homogeneous growth process it is not necessary for the concept of the «state of development» or for an equivalent one to be included in the set of the basic assumptions made on the model. However, in the solution of the model there appears an integral expression which we, in describing the behavior of the model, can with good reason call the «physiological clock» and, similarly, the values of the expression can be called the «state of development» or the «physiological age». As a matter of fact, we can show that if the growth process is in a proper way interpreted to be a general process with cardinal phases, the integral expression in question will be identical with the physiological clock defined in 2.4.

The semihomogeneous growth process is a natural generalization of the homogeneous growth process from which it follows that the «physiological clock» of the homogeneous process appears also in the formula of the semihomogeneous growth function.

Thus, in the formulas of the growth functions of the homogeneous and the semihomogeneous processes, there appears an integral expression whose values may be called the «physiological age» or equivalent. However, all the components of this integral expression can be computed directly from (appropriate) observational data (as can all the other parts of the growth function). Therefore, it is not necessary to make any a priori assumptions on the form of this integral expression, its formula or its numerical values.

5. HOMOGENEOUS GROWTH PROCESS

5.1. We now wish to find, for the growth process, a condition restrictive enough to enable the growth function formula to be easily derived and easily computed from observational data. A condition of this kind can be brought about if we require that the differential equation of the growth function should be separable, i.e. it should be of a well-known, easily solvable form. We choose this condition as our starting point but present the separability requirement in a somewhat unusual form and call it the *homogeneity condition*. Below, we shall show that the homogeneity we are to define is, when appropriately interpreted, identical with the homogeneity of the general process presented in Definition 3.3 in Chapter 3.

We introduce the following notation. Let $V_{z_0}(t)$ be the growth function corresponding to the basic state z_0 of the environment. Then $V_{z_0}(t) > 0$ for all $t \geq 0$, and thus $V_{z_0}(t)$ is a strictly increasing function with an inverse function which is denoted by $V_{z_0}^{-1}(x)$, as usual, or in other words, $V_{z_0}(V_{z_0}^{-1}(x)) = x$ for all $x \geq 0$.

5.2. DEFINITION. A growth process is called *homogeneous* if its growth function $V(t)$ satisfies the following condition:

$$(5.3) \quad \frac{V'_E(t)}{V_{z_0}(s(t))} = h(E(t)), \quad t \geq 0,$$

for all environmental functions E , where $s(t) = V_{z_0}^{-1}(V_E(t))$ and the function $h: \mathbb{R}^n \rightarrow \mathbb{R}$ is a continuous function depending only on the growth process itself. The function h is called the *homogeneity function* of the process.

For the sake of brevity, we also call the growth function $V(t)$ homogeneous and the function h its homogeneity function, if $V(t)$ is the growth function of a homogeneous growth process and h the homogeneity function of this process.

5.4. THEOREM. If V is a homogeneous growth function and h its homogeneity function, then V takes the form

$$(5.5) \quad V(t) = V_{z_0}(s(t)) \text{ where}$$

$$(5.6) \quad s(t) = \int_0^t h(E(r)) \, dr.$$

PROOF. We denote $F(t) = V_{z_0}(t)$, $t \geq 0$, and $G(x) = F^{-1}(x)$, $x \geq 0$, i.e. G is the inverse function of F . Further, let $v(x) = V'_{z_0}(V_{z_0}^{-1}(x)) = F'(G(x))$, $x \geq 0$. Then, due to condition (5.3), the growth function $V(t) = V_E(t)$ satisfies the differential equation $\frac{dV}{dt} = h(E(t)) v(V)$, from which, by 'separating the variables', we obtain $\frac{dV}{v(V)} = h(E(t)) dt$. By integrating both sides of this equation we obtain

$$(5.7) \quad \int_0^V \frac{dV}{v(V)} = \int_0^t h(E(t)) dt = s(t).$$

On the other hand, by the formula of the derivative of an inverse function $G'(x) = 1/F'(G(x))$, $x \geq 0$. Then

$$(5.8) \quad \int_0^V \frac{dV}{v(V)} = \int_0^V \frac{dV}{F'(G(V))} = \int_0^V G'(V) dV = G(V).$$

Now the equations (5.7) and (5.8) imply: $G(V) = G(V(t)) = s(t)$ and so $V(t) = F[G(V(t))] = F(s(t))$. Q.E.D.

Next, we shall prove a couple of equivalent conditions for the homogeneity of a growth function.

5.9. THEOREM. A growth function $V = V(t)$ is homogeneous if and only if it takes the form

$$(5.10) \quad V'(t) = f(E(t))g(r(t)), \quad t \geq 0, \text{ with}$$

$$r(t) = \int_0^t f(E(t)) dt,$$

where f and g are continuous functions and $f(z_0) > 0$. In particular, then $h = \frac{1}{f(z_0)} f$ is the homogeneity function of V .

PROOF. If $V(t)$ is homogeneous with h as its homogeneity function, then it clearly satisfies condition (5.10) by Theorem 5.4, because $h(z_0) = 1$ due to equation (5.3). On the other hand, let $V(t)$ be a growth function such that (5.10) holds for continuous functions f and g . Let G be the integral function of g with $G(0) = 0$, i.e. $G'(x) = g(x)$ for all $x \geq 0$. Observe that $\frac{d}{dt} r(t) = f(E(t))$ for all $t \geq 0$. Then it follows that

$$(5.11) \quad V(t) = \int_0^t \frac{dV}{dt} dt = \int_0^t f(E(t)) g(r(t)) dt \\ = \int_0^t \frac{d}{dt} G(r(t)) dt = G(r(t)), t \geq 0.$$

So, in particular, $V_{z_0}(t) = G(f(z_0)t)$, $t \geq 0$, which implies $G(x) = V_{z_0}(x/f(z_0))$, $x \geq 0$. Then we get

$$g(x) = G'(x) = \frac{1}{f(z_0)} V'_{z_0}(x/f(z_0)), x \geq 0,$$

and by (5.11), $V(t) = G(r(t)) = V_{z_0}(r(t)/f(z_0))$, which implies $r(t) = f(z_0) V_{z_0}^{-1}(V(t))$.

Thus (5.10) takes the form

$$V'(t) = f(E(t)) g(r(t)) = \\ f(E(t)) \frac{1}{f(z_0)} V'_{z_0}(r(t)/f(z_0)) = \\ \frac{f(E(t))}{f(z_0)} V'_{z_0} \left[\frac{1}{f(z_0)} f(z_0) V_{z_0}^{-1}(V(t)) \right] = \\ h(E(t)) V'_{z_0} \left[V_{z_0}^{-1}(V(t)) \right], t \geq 0,$$

with $h = \frac{1}{f(z_0)} f$. Hence the growth function $V(t)$ is homogeneous with h as its homogeneity function by Definition 5.2. Q.E.D.

5.12. THEOREM. The growth function $V(t)$ is homogeneous if and only if it satisfies the condition

$$(5.13) \quad V'(t) = u(E(t)) f(V(t)), t \geq 0,$$

where u and f are continuous functions with $u(z_0) > 0$ and $f(x) > 0$ for all $x > 0$, that is, the differential equation of $V(t)$ is separable.

PROOF. Obviously, a homogeneous growth function $V(t)$ satisfies condition (5.13). On the other hand, if $V(t)$ satisfies the separable differential equation (5.13), its solution takes, as is well-known, the form

$$(5.14) \quad V(t) = F(s(t)), \text{ where } s(t) = \int_0^t u(E(t)) dt,$$

and F is the inverse function of

$$G(x) = \int_0^x \frac{dt}{f(t)}, x \geq 0.$$

By differentiating both sides of (5.14) with respect to time t we obtain $V'(t) = u(E(t)) F'(s(t))$, and so $V(t)$ is homogeneous by Theorem 5.9. Q.E.D.

5.15. TESTING THE HOMOGENEITY OF THE GROWTH PROCESS AND COMPUTING THE GROWTH FUNCTION FROM EXPERIMENTAL DATA. Homogeneity can be tested directly with the aid of the defining condition (5.3), if numerous experimental data are available. It is then to be checked that the ratio of the derivatives $V'_E(t)$ and $V'_{z_0}(s(t))$ depends only on the state $E(t)$ of the environment at time t but not in any other way on the environmental function E or on the amount $V(t)$ of growth at time t . The value of this ratio $h(E(t))$ yields, as a byproduct, the values of the function h , whenever the ratio can be computed for a sufficient number of states z of the environment.

However, a considerably more practical and accurate way to test homogeneity and to compute the homogeneity function h is the following. We assume that functions $V = V_z(t)$ have been determined experimentally for a sufficient number of constant states z of the environment. If the process is homogeneous, then by Theorem 5.4

$$(5.16) \quad V_z(t) = V_{z_0}(h(z)t) \text{ for all } t \geq 0,$$

because, whenever the environment is in a constant state z all the time,

$$s(t) = \int_0^t h(z)dt = h(z)t.$$

We now must examine whether or not the experimentally determined functions $V_z(t)$ satisfy equation (5.16) for all z and all $t \geq 0$. This examination can be carried out graphically in several ways by comparing, in some appropriate way, the growth curves $y = V_z(x)$ with one another for different values of z . In the following, we shall present one method.

If (5.16) holds, then for a fixed z we get

$$(5.17) \quad h(z) = \frac{1}{t} V_{z_0}^{-1}(V_z(t))$$

for all $t \geq 0$. If the right hand side of (5.17) is constant for different values of t , this constant is $h(z)$ and equation (5.16) holds for the studied state z of the environment. When all states z of the environment are studied in this way the validity of (5.16) gets checked and, at the same time, the function h gets computed from the experimentally determined growth curves. If the right hand side of (5.17) is not independent of t , the growth process in question is not homogeneous.

On the other hand, if the relationship between $V_z(t)$ and $V_{z_0}(t)$ is in agreement with equation (5.16), the growth process is apparently homogeneous (cf. Remark 6.12). In order to make sure that this is the case it is necessary to test condition (5.3) by means of the function h which is already known. If the process proves homogeneous its growth function agrees with equation (5.5). The functions $V_{z_0}(t)$ and $h(z)$ in this equation have already been determined above.

As an example of testing the homogeneity of the growth function V and of determining the homogeneity function h we consider the following hypothetical situation. Let P be a growth process whose progress depends, in addition to time, on one environmental factor only, for instance, temperature T . Then $E(t) = T(t)$ for all $t \geq 0$. Assume that temperature $T_0 = 10^\circ\text{C}$ has been chosen as the basic state of the environment. Further, assume that the growth curves $y = V_T(x)$ for $T = 3, 6, 8, 10, 12, 15,$ and 20°C have been experimentally de-

termined. Let these curves agree with those in Fig. 1. Then the graph of the inverse function $V_{T_0}^{-1}(t)$ of $V_{T_0}(t)$ is presented in Fig. 2. From equation (5.17) the function h can be computed. Its graph is presented in Fig. 3. Finally, it can be established by computation (and graphically) that the functions in Fig. 1 satisfy equation (5.16) and that the process is obviously homogeneous.

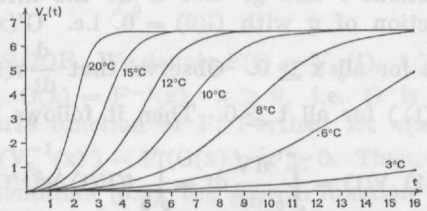


Figure 1. Example of growth curves $y = V_T(t)$ in constant temperatures $T = 3, 6, 8, 10, 12, 15$ and 20°C .

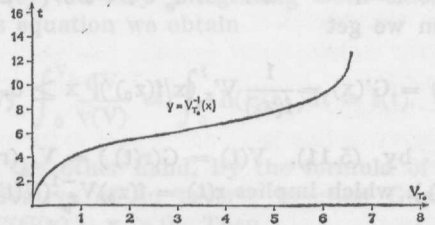


Figure 2. The graph of the inverse function of $V_{T_0}(t)$, $T_0 = 10^\circ\text{C}$.

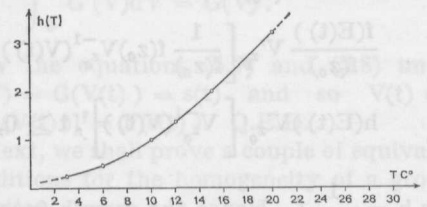


Figure 3. The graph of the homogeneity function $h(T)$.

5.18. REMARK. We now wish to show that the Definition (5.2) of the homogeneity of the growth function is in agreement with the definition of the homogeneity

of a general process (3.3). For this purpose, the growth process must first be interpreted, in an appropriate way, to be a general process whose progress is followed with the aid of the cardinal phases instead of the values of the growth function $V(t)$. This interpretation we make in a trivial way: we define that the different values $V(t)$, $t \geq 0$, assumed by the growth function V form the cardinal phases of a growth process. Then, according to the definition of the physiological age (2.2), the physiological age $s(t)$ of the growth phase $V(t)$ is the time required for the attainment of this amount of growth when the environment remains in the basic state z_0 all the time, that is, $s(t) = V_{z_0}^{-1}(V(t))$. Hence, by Definition 2.4 the expression of the physiological clock of the homogeneous growth process under consideration is $C(t, E) = V_{z_0}^{-1}(V_E(t))$. According to Remark 3.11, a general process is homogeneous and h its homogeneity function if and only if

$$\frac{d}{dt} C(t, E) = h(E(t)). \text{ Now,}$$

$$\begin{aligned} \frac{d}{dt} C(t, E) &= \frac{d}{dt} (V_{z_0}^{-1}(V_E(t))) = \\ &= (V_{z_0}^{-1})'(V_E(t)) V'_E(t) = \\ &= \frac{1}{V'_{z_0}(V_{z_0}^{-1}(V_E(t)))} V'_E(t), \end{aligned}$$

which means, $\frac{d}{dt} C(t, E) = h(E(t))$ if and only if

$$\frac{V'_E(t)}{V'_{z_0}(s(t))} = h(E(t)) \text{ with } s(t) = V_{z_0}^{-1}(V_E(t)).$$

Thus the definitions of homogeneity (3.3) and (5.2) are equivalent.

Note, especially, that if $V(t)$ is homogeneous, then by formulas (5.5) and (5.6) of Theorem 5.4, the formula of the physiological age is

$$s(t) = V_{z_0}^{-1}(V_E(t)) = \int_0^t h(E(t)) dt$$

and so we have for the physiological clock $V_{z_0}^{-1}(V_E(t)) = C(t, E)$,

$$C(t, E) = \int_0^t h(E(t)) dt.$$

Thus, the integral $\int_0^t h(E(t)) dt$ in formula (5.5) can be called the physiological clock of the homogeneous growth process P and its values $s(t)$ the physiological age of P at time $t \geq 0$.

5.19. REMARK. We shall show that the growth model used by POHJONEN (1975) is homogeneous. He investigates the growth of Italian ryegrass and the growth function involved is $W(t)$, where $W(t) =$ the dry weight of the yield at time t . The environmental function he denotes by $X(t)$, $t \geq 0$. The following assumption is made on the growth rate of the growth function (POHJONEN 1975, page 96, formula 4.7)

$$\frac{dW}{dt} = M(X(t))v(\bar{s}(t)), \text{ where } \bar{s}(t) = \int_0^t M(X(t)) dt, t \geq 0.$$

Here, $M: \mathbb{R}^n \rightarrow \mathbb{R}$ is a continuous function, a so-called «development rate», and $v(x)$, $x \geq 0$, is another continuous function, a so-called «proper growth rate». Both functions are independent of the environmental function $X(t)$.

Thus, by Theorem 5.9 the growth function $W(t)$ is homogeneous with $h = \frac{1}{M(z_0)} M$ as its homogeneity function, where z_0 is a (suitably fixed) basic state of the environment. Then by Theorem 5.4 the growth function $W(t)$ takes the form

$$W(t) = W_{z_0} \left(\frac{1}{M(z_0)} \bar{s}(t) \right),$$

where $W_{z_0}(t)$ is the growth function corresponding to the basic state z_0 . The function $h = \frac{1}{M(z_0)} M$ can be determined from (appropriately collected) observational data in accordance with the method described in Section 5.15.

5.20. GENERALIZATION OF THE HOMOGENEOUS GROWTH PROCESS. If $V(t)$ is the growth function of a homo-

geneous growth process, then by Theorem 5.4

$$(5.21) \quad V_z(t) = V_{z_0}(h(z)t), \quad t \geq 0,$$

for all constant states z of the environment. We consider the behavior of the growth during a long growing time, that is when $t \rightarrow \infty$. Let

$$\lim_{t \rightarrow \infty} V_{z_0} = L < \infty.$$

Then by (5.21)

$$(5.22) \quad \lim_{t \rightarrow \infty} V_z(t) = L$$

for all constant states z of the environment with $h(z) > 0$. Thus in all non-static constant states z of the environment, growth attains the same maximal growth L as a result of a long growing time. Obviously, this need not be the situation in a general nonhomogeneous growth process but rather, the size of the maximal growth $L(z)$ in a constant state z can also depend on the state z . We shall now find out how a shift could be accomplished, with a minimum of change, from a homogeneous to such a non-homogeneous case in which the maximal growth $L(z)$ could vary with z .

Let P be a growth process whose growth function in a constant state z takes the form

$$(5.23) \quad V_z(t) = \frac{L(z)}{L(z_0)} V_{z_0}(h(z)t), \quad t \geq 0$$

where $0 < L(z_0) < \infty$. Hence, $\lim_{t \rightarrow \infty} V_z(t) = L(z)$. We differentiate both sides of (5.23) with respect to time t and get

$$(5.24) \quad V'_z(t) = \frac{L(z)}{L(z_0)} h(z) V'_{z_0}(h(z)t) = u(z) V'_{z_0}(s(t)),$$

where we have written: $u(z) = L(z)h(z)/L(z_0)$ and $s(t) = h(z)t$. If we finally require that the growth rate $V'(t)$ of the growth function $V(t)$ is to take the form (5.24) not only in the constant states z of the environment, but also when the state of the environment varies, we arrive at the following requirement:

$$(5.25) \quad V'_z(t) = u(E(t)) V'_{z_0}(s(t)) \quad \text{with } s(t) = \int_0^t h(E(t)) dt$$

for all environmental functions $E(t)$ and all $t \geq 0$, where u and h are continuous non-negative functions.

If the growth function $V(t)$ of a growth process P satisfies condition (5.25), its behavior in the constant environmental states z is, short of the constant multiplier $L(z)/L(z_0)$, similar to that of a homogeneous growth function, but its maximal growth $L(z)$ in the constant state z depends on the state z . We call a growth process that satisfies condition (5.25) *semihomogeneous* and shall study it more closely in the next chapter.

6. SEMIHOMOGENEOUS GROWTH PROCESS

6.1. DEFINITION. A growth process is called *semihomogeneous* if its growth function takes the form

$$(6.2) \quad V'_E(t) = u(E(t))V'_{z_0}(s(t)) \text{ with } s(t) = \int_0^t h(E(t)) dt$$

for all $t \geq 0$ and for all environmental functions $E(t)$, where u and h are continuous functions such that $u(z) \geq 0$ and $h(z) \geq 0$ for all environmental states $z \in R^n$.

6.3. We also call the growth function of a semihomogeneous growth process *semihomogeneous*. The functions h and u of Definition 6.1 we call, respectively, the homogeneity function and the sensitivity function of the growth process (and of its growth function $V(t)$, too).

We immediately see that semihomogeneity is a generalization of homogeneity: homogeneous are such semihomogeneous processes for which $u = h$. From Definition 6.1 we directly get the formula of a semihomogeneous growth function by integrating both sides of equation (6.2):

6.4. THEOREM. If $V(t)$ is a semihomogeneous growth function, h its homogeneity function and u the sensitivity function, then the growth function $V(t)$ takes the form

$$(6.5) \quad V(t) = \int_0^t u(E(t))V'_{z_0}(s(t))dt \text{ with } s(t) = \int_0^t h(E(t))dt.$$

Furthermore, for the functions u and h the following holds:

$$(6.6) \quad u(z) = V'_z(0)/V'_{z_0}(0)$$

for all states z of the environment and, further,

$$(6.7) \quad V_z(t) = \frac{u(z)}{h(z)} V_{z_0}(h(z)t), \quad t \geq 0,$$

for all z such that $h(z) > 0$.

PROOF. Formula (6.5) is obtained directly from condition (6.2) by integration. For proving equation (6.7) let z be an arbitrary environmental state. If the environment is in a constant state z all the time, then

$$s(t) = \int_0^t h(z)dt = h(z)t, \quad t \geq 0.$$

Now, if $h(z) > 0$, then by (6.5)

$$\begin{aligned} V_z(t) &= \int_0^t u(z)V'_{z_0}(h(z)t)dt = \\ &= \frac{u(z)}{h(z)} \int_0^t \frac{d}{dt} [V_{z_0}(h(z)t)] dt = \\ &= \frac{u(z)}{h(z)} V_{z_0}(h(z)t), \end{aligned}$$

and so (6.7) holds. By differentiating (6.7) with respect to time t and putting $t = 0$ we get (6.6). In the case $h(z) = 0$, condition (6.5) implies

$$V_z(t) = \int_0^t u(z)V'_{z_0}(0)dt = u(z)V'_{z_0}(0)t, \quad t \geq 0.$$

By differentiating this equation with respect to t and putting $t = 0$ we get (6.6). Q.E.D.

6.8. THEOREM. Let $V(t)$ be a growth function such that

$$(6.9) \quad V'_E(t) = u(E(t))v(s(t)) \text{ with } s(t) = \int_0^t h(E(t))dt,$$

where u , v and h are continuous non-negative functions such that $u(z_0) > 0$ and $h(z_0) > 0$. Then $V(t)$ is semihomogeneous.

PROOF. Let $a = u(z_0)$ and $b = h(z_0) > 0$. Then (6.9) implies: $V'_{z_0}(t) = av(bt)$, and thus $v(t) = V'_{z_0}(t/b)/a$, $t \geq 0$. Then again by (6.9)

$$V'_E(t) = \frac{1}{a} u(E(t))V'_{z_0}\left(\frac{1}{b} s(t)\right)$$

for all environmental functions E and all $t \geq 0$, which implies that $V(t)$ is semihomogeneous by Definition (6.1). Q.E.D.

6.10. TESTING SEMIHOMOGENEITY AND COMPUTING THE GROWTH FUNCTION FROM EXPERIMENTAL DATA. Suppose that it has been possible to determine experimentally the growth curves $y = V_z(x)$ for a sufficient number of states z of the environment. We now wish to test the semihomogeneity of growth function $V(t)$ and compute its sensitivity function u and homogeneity function h by means of these growth curves. If $V(t)$ is semihomogeneous, we shall in this way manage to determine u and h . If $V(t)$ is not semihomogeneous, this is likely to show up as nonvalidity of equations (6.7) when functions u and h are being computed.

Consider growth curves $y = V_z(x)$ and $y = V_{z_0}(x)$. We determine values $u(z)$ and $h(z)$ from these curves. This can be done in several ways, for instance, as follows. For the sake of brevity, we denote $f(x) = V_{z_0}(x)$ and $g(x) = V_z(x)$ for all $x \geq 0$. Then by equation (6.7)

$$g(x) = \frac{u(z)}{h(z)} f(h(z)x), \quad x \geq 0.$$

We define two new functions, F and G , by equations

$$F(x) = \frac{f(2x)}{f(x)} \quad \text{and} \quad G(x) = \frac{g(2x)}{g(x)}, \quad x > 0.$$

The graphs of the functions F and G can be easily drawn with the aid of the graphs of $y = f(x)$ and $y = g(x)$. On the other hand,

$$G(x) = \frac{g(2x)}{g(x)} = \frac{f(2h(z)x)}{f(h(z)x)} = F(h(z)x)$$

for all $x > 0$. The value $h(z)$ can now be easily determined from curves $y = F(x)$ and $y = G(x)$ by comparing these curves with each other. For instance, choose an appropriate number $x_1 > 0$ and find x_2 such that $F(x_2) = G(x_1)$. If there are several x_2 to choose from, the 'correct' one is easy to distinguish. Then $F(x_2) = G(x_1) = F(h(z)x_1)$ and so $x_2 = h(z)x_1$ or $h(z) = x_2/x_1$. The value $h(z)$, of course, is to be computed

by means of several pairs (x_1, x_2) and the final $h(z)$ is to be determined, for instance, as the mean value of several results. Lastly, $u(z)$ is to be computed from the formula $u(z) = h(z)g(x)/f(h(z)x)$ with an appropriate value (or values) of x .

The method described above is illustrated by Figs. 4 and 5. The (hypothetical) functions $y = f(x)$ and $y = g(x)$ appear in Fig. 4 and the functions $y = F(x)$ and $y = G(x)$ computed from f and g , in Fig. 5. For determination of the value $h(z)$, $x_1 = 5$ has been chosen. From Fig. 5 it can be seen that $F(4) = G(5)$. Thus, $x_2 = 4$. So, $h(z) = 4/5 = 0.8$. For computation of the value $u(z)$, $x = 7$ has been chosen and then we get $u(z) = h(z)g(7)/f(h(z)7) = 0.8 g(7)/f(5.6) = 0.6$.

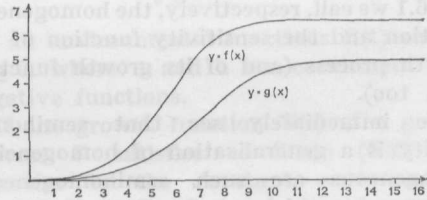


Figure 4. The graphs of the functions f and g .

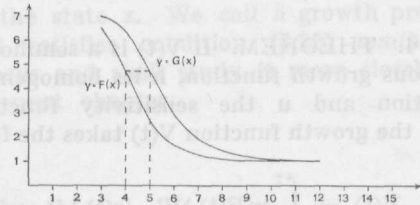


Figure 5. Determining $h(z)$ from the graphs of F and G .

When the functions u and h have in this way been determined from experimental data, it is necessary to check how well equation (6.7) holds for the different states z of the environment. If it does not hold at all, the growth process under consideration is not semihomogeneous. If (6.7) holds satisfactorily, the process is apparently semihomogeneous, cf. Remark 6.12. However, for final ascertainment of the semihomogeneity it is necessary to check by

means of observational data whether or not the defining condition (6.2) holds for a sufficient number of environmental functions. Here $s(t)$ can now be computed with the aid of the homogeneity function h determined above. If the growth function $V(t)$ proves to be semihomogeneous, it is possible that it may even be homogeneous. Namely, if $u = h$, $V(t)$ is homogeneous and the formula of its growth function is obtained from equation (5.5). If $V(t)$ is semihomogeneous, but the functions u and h distinctly differ from each other, the growth function $V(t)$ complies with formula (6.5).

6.12. REMARK. If $V(t)$ is semihomogeneous (or homogeneous, whence $u = h$), then it is necessary, by Theorem 6.4, that

$$(6.13) \quad V_z(t) = \frac{u(z)}{h(z)} V_{z_0}(h(z)t), \quad t \geq 0,$$

for all states z of the environment. This gives rise to the question: is the validity of equation (6.13) also a sufficient condition for semihomogeneity? In other words, if the growth curves $y = V_z(x)$ have been determined experimentally and the functions u and h have been computed from these curves and the equation (6.13) has proved to hold for all z , is the growth function $V(t)$ necessarily semihomogeneous?

In view of the biological nature of the growth process, the answer is inclined to be affirmative, which would mean that (6.13) is also a sufficient condition for semihomogeneity. So far, the author has not been able to prove this. However, this view finds support in the following.

Consider two growth processes P and P^* whose growth functions are $V(t)$ and $V^*(t)$. We assume that they progress exactly in the same way whenever the environment is in a constant state z all the time, and this holds for any z , i.e.

$$(6.14) \quad V_z(t) = V_z^*(t) \quad \text{for all } t \geq 0 \quad \text{and} \\ \text{for all } z.$$

Now it seems natural to conclude that P and P^* always progress in the same way, even when the environmental state varies during the process, i.e.

$$(6.15) \quad V_E(t) = V_E^*(t)$$

for all $t \geq 0$ and for all environmental functions E .

In order to formulate, more clearly, the above problem that remains open, we define that a set \mathcal{P} of growth processes is called *normal* if the two conditions below are satisfied:

a) For any two growth processes P and P^* in \mathcal{P} the following holds: if P and P^* satisfy condition (6.14), then they inevitably satisfy condition (6.15), too.

(b) The set \mathcal{P} contains all the semihomogeneous growth processes.

From a biological point of view, the assumption that the set of growth processes under consideration is normal seems a rather slight restriction. If this assumption can be made, it leads to a considerable advantage: the validity of equation (6.13) alone guarantees that the growth process is semihomogeneous.

Consequently, it would be of great value for the mathematical research on growth processes to find a condition that is as general as possible and guarantees normality in the above sense.

6.16. REMARK. To conclude with we shall show that the growth model used by HARI et al. (1970 and 1974) is semihomogeneous. Their model is based on the following assumptions. As regards environmental factors, only temperature T is assumed to affect (appreciably) the growth process under consideration, that is, $E(t) = T(t)$, $t \geq 0$. The growing season has been divided into days in such a way that the j :th day begins at time t_j , $j = 1, 2, \dots$, and $t_1 = 0$. It is then assumed (HARI et al. 1970, page 377, formulas (8) and (9)):

$$(6.17) \quad \int_{t_j}^{t_{j+1}} \frac{dV}{dt} dt = g_j \approx f(s_j)a(r_j + b),$$

where a and b are constants, f a continuous non-negative function and $s_j = s(t_j)$, $r_j = s(t_{j+1}) - s(t_j)$ with

$$s(t) = \int_0^t R(T(t)) dt, \quad t \geq 0.$$

Here $R(T)$ is a fixed continuous non-negative function. From assumption (6.17) it follows:

$$f(s_j)a(r_j + b) = f(s_j)a \left(\int_{t_j}^{t_{j+1}} R(T(t)) dt + b \right)$$

$$b) = af(s_j) \int_{t_j}^{t_{j+1}} (R(T(t)) + c) dt \approx \int_{t_j}^{t_{j+1}} a(R(T(t)) + c)f(s(t)) dt,$$

where $c = b/(t_{j+1} - t_j)$. Thus, it follows from assumption (6.17)

$$V(t_k) = \int_0^{t_k} \frac{dV}{dt} dt = \sum_{j=1}^{k-1} \int_{t_j}^{t_{j+1}} \frac{dV}{dt} dt \approx \sum_{j=1}^{k-1} \int_{t_j}^{t_{j+1}} a(R(T(t)) + c)f(s(t)) dt = \int_0^{t_k} a(R(T(t)) + c)f(s(t)) dt$$

for all $k = 1, 2, \dots$. Then we may assume that the above result is valid with equality signs for all $t \geq 0$, that is,

$$V(t) = \int_0^t a(R(T(t)) + c)f(s(t)) dt, t \geq 0.$$

By differentiating both sides of this equation with respect to time t we get

$$(6.18) \quad \frac{dV}{dt} = a(R(T(t)) + c)f(s(t)).$$

Therefore, the growth function $V(t)$ is semihomogeneous with $u(T) = a(R(T) + c)$ as its sensitivity function and $R(T)$ as its homogeneity function. Consequently, $u(T)$ and $R(T)$ satisfy equation (6.7) for all temperatures T . Furthermore, they can be computed from the experimental growth curves $y = V_T(x)$ as described in Section 6.10.

On the other hand, by Theorem 5.9 the investigated growth function $V(t)$ is homogeneous if, in equation (6.18), the constant

c is equal to zero. As a matter of fact, the assumption $c \neq 0$ does not seem very natural. Namely, if $c < 0$ and, at some temperature T , the inequality $R(T) < |c|$ would hold, then at that temperature growth would go backwards ($a > 0$, of course)! Also, if $c > 0$, then the rate of growth $\frac{dV}{dt}$ never drops below the positive limit $acf(s(t))$, not even at very low temperatures T .

However, satisfactory results have been obtained (HARI et al. 1970 and 1974) with the above model based on the assumption (6.17) with $b \neq 0$ (that is, $c \neq 0$, too). Furthermore, the value of b has depended on the growth process under investigation and has always deviated considerably from zero. This can be explained as follows.

If in equation (6.18) the homogeneity function $R(T)$ is replaced by the homogeneity function $R^*(T) = R(T) + c$, (6.18) takes the equivalent form

$$(6.19) \quad \frac{dV}{dt} = R^*(T(t)) af(s^*(t) - tc) \quad \text{with} \quad s^*(t) = \int_0^t R^*(T(t)) dt.$$

Since $|c|$ in any case is a small number, it seems obvious (within the limits of satisfactory accuracy) that in equation (6.19) the expression $af(s^*(t) - tc)$ can be replaced by $v(s^*(t))$, where $v(x)$ is an appropriate (fixed) continuous function. If this replacement is possible, equation (6.18) takes the form

$$\frac{dV}{dt} = R^*(T(t))v(s^*(t)).$$

Then, by Theorem 5.9, the growth function $V(t)$ is homogeneous and the formal difficulties pertaining to the constant c in equation (6.18) are eliminated. Also, if $V(t)$ is really homogeneous, the computation of its formula from the experimental growth curves will be simplified.

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Seloste:

FYSIOLOGISEN KELLON JA KASVUN MATEMAATTINEN MALLI

Fysiologisen kellon käsitettä käytetään kuvailemalla biologisen kehitys- tai kasvuprosessin kulkua. Tällöin prosessin kulun ajatellaan riippuvan, mahdollisesti muiden tekijöiden ohella, prosessille ominaisesta fysiologisesta kellosta, jonka 'käynti' saattaa huomattavasti poiketa tavallisen kellon käynnistä. Esimerkiksi erilaisia lämpösumma-menettelyjä on usein käytetty tällaisina fysiologisina kelloina.

Käsillä olevan tutkimuksen tarkoituksena on antaa fysiologiselle kellolle täsmällinen määritelmä ja tutkia matemaattisesti sen roolia kehitys- ja kasvuprosesseissa.

Työn alkupuolella (luvut 1–3) tarkastellaan fysiologista kelloa. Lähtökohtana on tällöin RISTO SARVAKSEN (1972–1974) metsäpuiden vuotuisen kehityssyklin tutkimisessa käyttämä lämpösummamenetelmä. Hänen määrittelemässään muodossa lämpösumma on integraalilauseke, jonka kaava määrätään kokeellisesti tutkittavasta kohteesta. Käsillä olevassa työssä analysoidaan, mitkä ovat tämän lämpösummamenetelmän matemaattiset perusteet sekä esitetään kuinka yleinen fysiologinen kello saadaan toimimaan samoilla periaatteilla. Aiheen käsittely on pääpiirteittäin seuraava.

Tarkastellaan ensin yleistä prosessia, joka koostuu ketjusta peräkkäisiä tapahtumia, mutta mihin ei välttämättä alunperin liity mitään numeerista asteikkoa. Prosessin edistymisen oletetaan riippuvan ajasta ja ympäristöolosuhteista prosessin aikana. Tällaisia ympäristötekijöitä voivat olla esimerkiksi lämpötila, kosteus, valaistus, maaperän laatu jne. Esimerkiksi metsäpuiden vuotuinen kehityssykli on eräs tällainen prosessi.

Seuraavaksi määritellään prosessin fysiologisen kellon käsite. Se tulee olemaan, pyöreästi sanoen, matemaattinen kaava, josta voidaan laskea, missä kehitysvaiheessa prosessi kullakin hetkellä on, kun tunnetaan ympäristötekijät ja niiden vaihtelu ajan suhteen prosessin aikana.

Varsinaisen matemaattisen ja myös käytännöllisen ongelman muodostaa kysymys, miten prosessin fysiologisen kellon kaava voidaan johtaa ja kokeellisista havaintoarvoista yksityiskohtaisesti määrätä. Yleisessä tapauksessa tehtävä voi olla ylipääsemättömän vaikea. Kuitenkin jos prosessi täyttää jonkin tilannetta riittävästi yksinkertaisen

tavan lisäehdon, voidaan etsitty kaava löytää. Erään tällaisen lisäehdon toteuttaa esimerkiksi metsäpuiden vuotuinen kehityssykli ja tässä kirjoituksessa kyseistä ehtoa kutsutaan *homogeenisuusehdoksi*. Jos prosessi toteuttaa kyseisen ehdon, kutsutaan sitä *homogeeniksi*. Prosessin homogeenisuus voidaan kokeellisesti testata (ainakin periaatteessa) yksinkertaisin koejärjestelyin.

Esillä olevassa tutkimuksessa saadaan seuraava fysiologista kelloa koskeva päätulos: Jos prosessi on homogeeninen, voidaan sen fysiologisen kellon lausekkeen yleinen muoto helpolla johtaa ja (sopivasti kerätyistä) kokeellisista havaintoarvoista tämän lausekkeen yksityiskohdat laskemalla määrätä.

Erityisesti lämpösummaan sovellettuna tästä päätuloksesta seuraa, että jos lämpötila on ajan ohella ainoa homogeenin prosessin kulkuun vaikuttava ympäristötekijä, niin sen fysiologisen kellon lauseke on samaa muotoa kuin R. SARVAKSEN (1972) esittämä lämpösumma-integraali, ja mielekästä (s.o. tietyt normitusehdot täyttävää) lämpösummaa ei voida millään muulla tavalla laskea.

Työn jälkimmäisessä osassa (luvut 4–6) tarkastellaan kasvuprosesseja. Kasvuprosessille on ominaista, että siihen liittyy jokin ajan mukana kasvava numeerinen suure $V = V(t)$, jonka arvo kullakin hetkellä kuvaa prosessin kasvuvaihetta. Prosessin etenemisen oletetaan riippuvan ajan ohella myös ympäristötekijöistä, joten $V(t)$ on sekä ajan että ympäristön tilan funktio. Funktiota $V(t)$ kutsutaan prosessin *kasvufunktioksi*. Esimerkiksi puun pituuskasvu on kasvuprosessi ja sen kasvufunktio saadaan asettamalla $V(t) =$ puun pituus hetkellä t .

Kasvuprosessin hallitsemiseksi riittää tuntea sen kasvufunktion $V(t)$ lauseke eli kaava. Jälleen yleisessä tapauksessa kasvufunktion kaavan johtaminen voi olla hyvin vaikeaa. Kuitenkin jos kasvuprosessi toteuttaa jonkin tilannetta riittävästi yksinkertaisen lisäehdon, voidaan sen kaava löytää. Tässä työssä esitetään kaksi tällaista lisäehtoa kasvuprosesseille, *homogeenisuus*- ja *semihomogeenisuusehdot*, sekä johdetaan kumpaakin ehtoa vastaavan kasvufunktion kaava. Lisäksi esitetään, miten kokeellisesti voidaan testata, toteuttaako tarkasteltu kasvuprosessi jomman kumman näistä ehdoista. Edelleen osoitetaan,

miten kokeellisista havaintoarvoista voidaan määrätä vastaavan kasvufunktion eri osat yksityiskohtaisesti.

Homogeenisuus- tai semihomogeenisuusehdon täyttävälle kasvuprosessille johdettu kasvufunktion kaava paljastaa mielenkiintoisen yhteyden työn alkupuolella määriteltyyn fysiologiseen kelloon. Kaava nimittäin sisältää kummassakin ta-

pauksessa integraalilausekkeen, joka osoittautuu olevan kyseisen kasvuprosessin fysiologinen kello. Jos tämän integraalilausekkeen arvoa kullakin hetkellä (prosessin ollessa käynnissä) kutsutaan kasvuprosessin (tai kyseisen kasvavan kohteen) fysiologiseksi iäksi, on löydetty täsmällinen tulkinta kasvun riippuvuudelle ajasta, ympäristöolosuhteista ja kasvavan kohteen fysiologisesta iästä.

SARVAS, JUKKA

O.D.C. 161.4 + 181.65 — — 015.5

1977 Mathematical model for the physiological clock and growth.
ACTA FORESTALIA FENNICA 156. 25 p. Helsinki.

In this paper a precise definition is given of the term physiological clock and the role of this clock in biological developmental and growth processes is mathematically studied. The heat sum method employed in the study of the annual cycle of development of forest trees has been used as the starting point. The mathematical principles of this method are analyzed and it is shown that, on the same principles, a fairly general physiological clock can be constructed. Also, two growth models are presented in which this generalized physiological clock proves to play an important role.

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kuusimetsän ravinnetilaan Pohjois-Suomessa (64° 28' N).

KANNATAJAJÄSENET — UNDERSTÖDANDE MEDLEMMAR

CENTRALSKOGSNÄMNDEN SKOGSKULTUR
SUOMEN METSÄTEOLLISUUDEN KESKUSLIITTO
OSUUSKUNTA METSÄLIITTO
KESKUSOSUUSLIIKE HANKKIJA
SUNILA OSAKEYHTIÖ
OY WILH. SCHAUMAN AB
OY KAUKAS AB
KEMIRA OY
G. A. SERLACHIUS OY
KYMIN OSAKEYHTIÖ
KESKUSMETSÄLAUTAKUNTA TAPIO
KOIVUKESKUS
A. AHLSTRÖM OSAKEYHTIÖ
TEOLLISUUDEN PUUYHDISTYS
OY TAMPELLA AB
JOUTSENO-PULP OSAKEYHTIÖ
KAJAANI OY
KEMI OY
MAATALOUSTUOTTAJAIN KESKUSLIITTO
VAKUUTUSOSAKEYHTIÖ POHJOLA
VEITSILUOTO OSAKEYHTIÖ
OSUUSPANKKIEN KESKUSPANKKI OY
SUOMEN SAHANOMISTAJAYHDISTYS
OY HACKMAN AB
YHTYNEET PAPERITEHTAAT OSAKEYHTIÖ
RAUMA-REPOLA OY
OY NOKIA AB, PUUNJALOSTUS
JAAKKO PÖYRY & CO
KANSALLIS-OSAKE-PANKKI
OSUUSPUU
THOMESTO OY