WORKING PAPER

MODEL OF THE OPTIMAL DEVELOPMENT
OF A PLANT TAKING INTO ACCOUNT
DEFENCE AND COMPETITION

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Foreword

This paper presents a very simple model of the development of a species, taking into account the energy expended on growth and on competition. Using probability distributions on growth rates and population densities, some very general results are obtained. The model predictions of course need to be tested with field data, and this may provide a conceptual framework for new measurement programs.

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Leader
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M.Ya. Antonovski, M.D. Korzukhin,* M.T. Ter-Mikhaelian*

1. INTRODUCTION

In this paper we formulate and investigate a particular development model of a plant, whose growth maximizes reproduction during the life cycle. In comparison with available models (a brief review follows), we have included in our model the competition between plants and the costs of an individual's defence. This connects the development problem with the problem of population dynamics.

A plant species we see now is the result of an evolutionarily formed genotype. It is doubtful whether it would be possible or desirable to restore the list of factors (with their densities and intensities), which had a significant influence on the present stage of development. A more realistic way of investigating development and its changes under different ecological conditions is to make hypotheses about these factors, to formulate models, and to test them with field data. The important factors in our model are the site quality (generalized resource) and population density.

2. LITERATURE REVIEW

There is a voluminous literature on the problem of optimal development (or life strategies) of plants and animals. We shall dwell on papers containing models most similar to ours.

We study a perennial (plant or tree), which divides available resources amongst a number of functions (the growth of various plant organs, adaptation to varying ecological conditions, defence from mortality factors). The problem of resource division is discussed in detail from the biological point of view in Pianka (1981). There exist two quite different approaches to tree growth modelling, namely, optimal and non-optimal models. The basic merit of the second class of model is that they are simpler from the experimental point of view, viz., comparing simulation results with field data. The merit of the first class of models is their greater biological validity and their consideration of the entire organism, which given an opportunity to describe one of its most important properties, namely, its ability to adapt. Two optimization principles (in different modifications) are commonly used - productivity optimization (increase in biomass) (Kibzun, 1983; Menjulin and Savvateev, 1981; Nilson, 1968; Oya, 1985; Oya, 1986; Racsko, 1979; Racsko, 1987; Tarko and Sadulloev, 1985) and maximization of the number of seeds or population growth rate (Antonovski and Semenov, 1978; Antonovski and Korzukhin, 1983; Vorotintsev, 1985; Insarov, 1975; Korzukhin, 1985; Semevski and Semyonov,

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1982; Tarko and Sadulloev, 1985; Hanin and Dorfman, 1973; Caswell, 1982). The second principle seems to be more valid from an evolutionary point of view (Pianka, 1981; Semevski and Semyonov, 1982; Hanin and Dorfman, 1980; Holden, 1935).

The main factors to be considered in a problem statement for optimal development are the following. (1) The partitioning of energy between growth and reproduction for a plant was considered in Vorotintsev, 1985; Insarov, 1975; Korzukhin, 1975; Tarko and Sadulloev, 1985. (2) The growth curve maximizing an animal's fertility taking into account its defence expenses was investigated in Hanin and Dorfman (1973); in fact it was the balance between growth and defence expenses that was investigated. (3) Plant competition was taken into account only in Korzukhin (1985), but population density was considered as an external parameter not as a dynamic variable. In Semevski and Semyonov (1982) for the first time a non-stepped reproductive curve was obtained; this result was achieved by including a stochastic mechanism in the model, namely, the probability of seed germination at each step of development. A similar curve was obtained in Tarko and Sadulloev (1985), but with simultaneous use of two nonintegral principles of optimization. In all other papers, only stepped reproductive curves were obtained. In Oya (1985), Oya (1986), Racsko (1979) and Racsko (1987), the purpose was to find a correlation between different plant organs, maximizing the increase in biomass on the next step; smooth growth curves were obtained.

To our knowledge a search was never made for a survival curve by means of optimal development models. The optimal correlation of growth and defence for an annual plant but for an arbitrary number of mortality factors was obtained in Semevski and Semyonov (1982).

There is also a number of models of a different type; in these models the fertility of vegetable cover as a whole is optimized, i.e., without considering separate individuals.

3. CONSTRUCTION OF THE MODEL

When attempting to construct a model of optimal growth of a tree, we would like first of all to obtain at least the main qualitative features of this growth (see fig.1): smooth growth of tree biomass $m(t)$, attaining some maximal value; reproductive curve $q(t)$ having no fruiting until some nonzero age t_0, increasing thereafter up to the end of life; decreasing t_0 with deteriorating ecological conditions; increasing t_0 with increasing population density; estimates in even-aged plantations of probability $p(t)$ of attaining age t (this probability is proportional to current density $n(t)$.

Since by means of variable $n(t)$ we in fact consider the population's dynamics, it is desirable also to describe in the model the behavior of the main population variables. In our case, $m(t)$ and $q(t)$ are variables of total biomass and total number of seeds for unit square of plantation - $M(t) = m(t)n(t)$ and $Q(t) = q(t)n(t)$. The behaviour of $M(t)$ and $Q(t)$ is usually nonmonotonous; for more detailed discussion of the variables of an even-aged population, see Korzukhin (1986).

Formulation of the general model.

Consider the population composed of n identical individuals, their life span being equal to N. Suppose that individuals consume only one type of resource; its maximum quantity accessible to one unit of plant's leaf surface is equal to a^{max}, real quantity is equal to $a < a^{max}$. The rate of net photosynthesis is equal to F. Assume that the seeds produced by individuals are kept during their life cycle; thus the population is always even-aged and its density is monotonously decreasing.
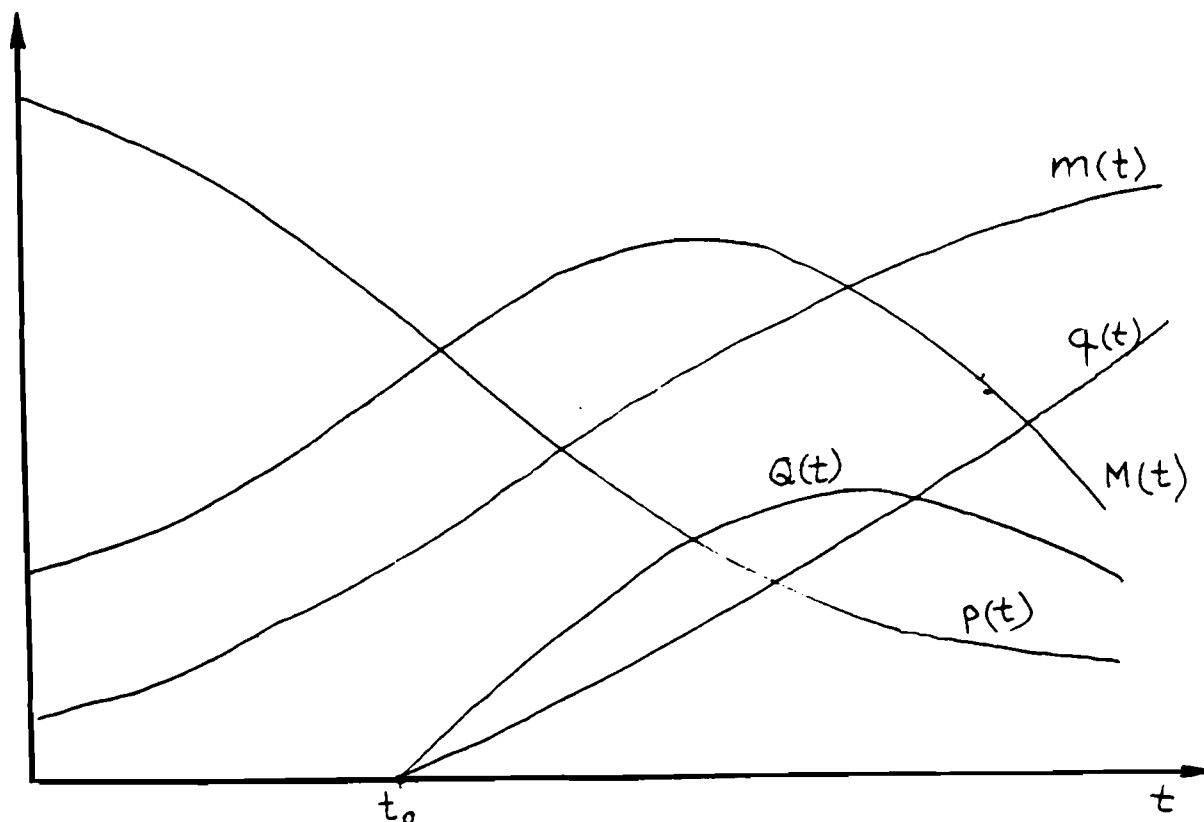
Figure 1:   Usual behaviour of variables describing dynamics of uneven-aged tree
population. t is age of population; $m(t)$ and $M(t)$ are biomasses of in-
dividuals and the population respectively; $q(t)$ and $Q(t)$ are biomasses
of total number of seeds produced by individuals and the population
respectively; $p(t)$ is an individual's probability of attaining age of t.

We shall take the simplest method of describing an individual's dynamics by one
variable, namely, the biomass m_i measured at discrete moments of time $i = 1,...,N$.
In order to take into account an individual's defence expenses, we include in the
model dynamic variable p_i denoting the probability of attaining age i; it is obvious
that $p_i = n_i / n_1$, where n_i is the population density at age i. Assume that an indi-
vidual spends fractions x_i, y_i, z_i of photosynthetic product on the defence from
mortality factors, biomass growth and reproduction, respectively,
$x_i + y_i + z_i = 1$. These fractions according to the optimization principle should

be found by maximizing the total number of seeds produced by an individual during its life cycle

$$R = \sum_{i=1}^{N} q(m_i, z\, F_i) p_i \ , \tag{1}$$

where q is the number of seeds produced at step i by an individual with biomass m_i in the case when its expenses on reproduction are equal to $z_i F$.

Let us discuss the equations describing the dynamics of biomass and population density (i.e., the probability of attaining age i). The first is the well known equation of organic substance balance for an individual

$$m_{i+1} = m_i + y_i F(m_i, a) - b(m_i) \ . \tag{2}$$

where F is the rate of photosynthesis at given biomass m_i and resource a, and b denotes the expense of respiration. Equation (2) in different modifications has been used repeatedly in growth models (Karev, 1985; Bugrovski et al., 1982; Oya, 1985; Racsko, 1979; Sirotenko, 1981).

The dependence of survival function V on the amount of resource a and the individual's parameters in the equation describing the dynamics of population density

$$n_{i+1} = V n_i \tag{3}$$

is known even more poorly than the form of F in (2). For example, we cannot answer definitely whether V is dependent on an individual's current state or on some part of its growth trajectory. The last assumption includes in the survival function something like "memory" and is quite possible from a physiological viewpoint. Later we shall take the simplest hypothesis about lack of "memory". It is also possible that V depends on an individual's biomass but without any information on the possible form of $V(m)$, we shall not use it.

According to the present state of survival theory (Semevski and Semyonov, 1982) the biomass depends on the pressure of the mortality factor V and the amount of resource r spent on defence. $V = V(W, r)$ (we consider the one-factor case; by "resource" we mean an individual's interior resource, i.e., the part of an individual's energy spent on defence); at the same time, V is a concave function of r. Let us use one of the possible ways to introduce resource (Antonovski et al., 1984; Korzukhin, 1986), namely

$$r = x F[m, a(n)] / F^{\max} \ , \tag{4}$$

where F is photosynthesis; x is the part of its production expended on defence; $a(n)$ is an ecological resource (e.g. light) accessible to the individual that depends on density n of population; $a^{\max} = a(0)$; $F^{\max} = F[m, a^{\max}]$ is the maximum rate of photosynthesis. Assume that in the case when an individual expends maximum accessible resource ($a = 1$, $F = F^{\max}$) on defence, the survival is a maximum, i.e., the individual is totally defended, $V(r=1) = 1$.

Let us discuss possible ways of including population density in the list of factors that have been influential in forming an individual's genotype. Consider an even-age population.

Judging by the present dynamics of boreal forests, the conclusion can be reached that most exogeneous disturbances almost completely destroy an initial stand (wildfires, windfalls, pests). In that case, an intensive invasion of free territory begins with a "package" of pioneer individuals that can be considered as even-aged (Kazimirov, 1971; Kirsanov, 1976); these individuals strongly interact with each other and depend only slightly on younger individuals of lesser size. So the following problem statements are possible.

It can be assumed that individual trees were formed at different initial densities of population $n^i(1)$ (each with its probability h^i); i is a number of initial conditions. In that case, the following quantity has to be optimized

$$R = \sum_i h^i \sum_k q_k[n^i(1)] ,\qquad(5)$$

where q_k is the number of seeds produced by an individual at age k.

It can be assumed that an individual tree was formed at one (or a group of closed values) initial density $n^*(1)$; this assumption is a particular case of (5). In this case, an individual's behaviour at initial densities different to $n^*(1)$ is suboptimal.

It can be assumed also that an individual was formed at different initial densities and was optimally adapted to each of them. The formalization of this viewpoint is similar to the previous one and leads to the maximization of the quantity

$$R = \sum_k q_k[n(1)] .\qquad(6)$$

Later on we shall use the simplest version (6).

Before writing the final version of the model, it is convenient to introduce specific photosynthesis f (per sq.cm.) for an individual instead of the total one F, and the individual's leaf surface S, so that

$$F = S \cdot f(S,a) .$$

The dependence $S(m)$ can be taken in the form $S \sim m^d, d < 1$ (Kuzmichev, 1977). (Dependence $f(S)$ appears through effects like crown self-shading).

The general form of the model to be suggested is:

$$n^{i+1} = V\left[\frac{x_i f(a)}{f^{max}(a)}\right] n_i ;\qquad(7)$$

$$m_{i+1} = m_i + y_i S(m_i) f(a) - b(m_i)\qquad(8)$$

$$R = \frac{1}{n_i} \sum_{i=1}^{N} q[z_i S(m_i) f(a), m_i] n_i \longrightarrow \max\qquad(9)$$

$$x_i + y_i + z_i = 1 ,$$

where $a(m_i, n_i)$ is the amount of accessible (per individual ecological resource in an even-aged population of n_i individuals with biomass m_i, $S(m_i)$ being equal to an individual's leaf surface. The parameters to be found are vectors (x, y, z) that provide a maximum value for function (9).

Let us describe the particular case of model (7)-(9) investigated in the present paper (one part of the investigation was made by means of analytical tools and the other by computer simulation). It was assumed that:

- the specific photosyntheses f is independent on leaf surface S (i.e., there is no crown self-shading);

- the resource accessible to an individual depends exponentially on the product $S \cdot n$ (in fact here we used the competition model developed in Korzukhin and Ter-Mikhaelian (1982) that contains an analytical deduction of this formula);

- leaf surface is proportional to biomass m (a simplified version with $d = 1$ in order to make the investigation easier);

- the survival V, firstly, depends on its argument in a linear manner and secondly assumes that an individual is able to defend itself totally from exogenous influences, i.e.,

$$V = u + (1-u)x_i ;$$

- the energy expended on respiration is proportional to total photosynthesis; i.e., in (8) $b \sim S \cdot f$;

- the number of seeds produced by an individual at one step (during one year) is proportional to total photosynthesis, i.e., q in (9) depends on its argument in a linear manner;

- specific photosynthesis f is proportional to the amount of accessible resource (in order to decrease the number of parameters).

As a result, we obtain

$$n_{i+1} = [u + (1-u)x_i]n_i ; \tag{10}$$

$$m_{i+1} = m_i + y_i m_i a e^{-lm_i n_i} ; \tag{11}$$

$$R = \frac{1}{n} \sum_{i=1}^{N} z_i m_i a e^{lm_i n_i} n_i \rightarrow \max ; \tag{12}$$

$$x_i + y_i + z_i = 1 ,$$

where l is an intensity of competition.

The parameter u is equal to survival in the case when an individual expends nothing on defence; otherwise it can be interpreted as a measure of site favourability for an individual.

4. SOME RESULTS.

The particular case of this model describing an individual's development without competition has been investigated by means of analytical tools; in fact this case describes the growth of a single individual

$$n_{i+1} = [u + (1-u)x_i]n_i \; ; \tag{13}$$

$$m_{i+1} = m_i + y_i \, a m_i \; ; \tag{14}$$

$$R = \frac{1}{n_1} \sum_{i=1}^{N} z_i a m_i n_i \rightarrow \max \; ; \tag{15}$$

$$x_i + y_i + z_i = 1 \, .$$

Here it is possible to consider a as an abstract parameter being dependent on some concrete ecological factor (e.g., on light in an hyperbolic manner). The discrete analogy of this model, investigated in Semevski and Semyonov (1982), can be obtained in the case of a maximum favourable environment, i.e., $u = 1$ (that means $n_i = n_1$).

Let us investigate the dependence of an individual's optimal strategies on parameters a and u, considering as usual R to be a function of $(x_N, y_N), \ldots, (x_1, y_1)$ where $k = 1, \ldots, N$ is the number of maximization steps. We mark the values of x, y, z, providing a maximum to functional R with upper indices. At each maximization step k, functional R is a quadratic function of variables x_{N-k}, y_{N-k}.

$$R(x_{N-k}, y_{N-k}) = R_{N-k-1} + C_{0,N-k} + C_{1,N-k}x_{N-k} \tag{16}$$
$$+ C_{2,N-k}y_{N-k} + C_{3,N-k}x_{N-k}y_{N-k} \, ,$$

where R_{N-k-1} are items of R depending on x, y with indices of lesser values than $N-k$. It follows from the right sides of equations (13), (14), that $C_{3N-k} > 0$ for all k; a concrete form of coefficients C_{j1} is determined by values of x, y providing a maximum to R at the foregong steps of optimization.

Since we consider function (16) within the triangle

$$x_{N-k} \geq 0, \; y_{N-k} \geq 0, \; y_{N-k} \leq 1 \, ,$$

it follows from $C_{3,N-k} > 0$ that a maximum can be reached either at

$$x^{N-k} = 0, \; y^{N-k} = 0 \, ,$$

or at some point of the segment

$$x^{N-k} + y^{N-k} = 1 \, . \tag{17}$$

Let us denote this local maximum R_k^{00} and R_k^{11}, respectively.

It is obvious that $z^N = 1$, $x^N = y^N = 1$. Consecutive maximization of functions of type (16) from $k = 1$ to $k = N-1$ gives the following results (technical details of this conclusion are obvious and therefore omitted).

Let $x_{N-k}^{\bullet}$, $y_{N-k}^{\bullet}$ denote values of x_{N-k}, y_{N-k} at which derivatives dR / dy_{N-k}, dR / dx_{N-k} are equal to zero.

Let us assume that at maximization steps $i = 1, \ldots, k-1$, a maximum of R has been reached in $x^{N-1} = y^{N-1} = 0$. The equation

$$au^{k+1} - (a+1)u + 1 = 0 ,$$ (18)

determines the curve $u_k^1(a)$ on which $x_{N-k}^{\bullet}(u,a)$ at maximization step k for the first time becomes equal to zero (being more than zero at the foregoing steps). It can be shown that at step k, the value $y_{N-k}^{\bullet}(u,a)$ is always more than 1.

On the curve determined by equation

$$u_0(a) = (1+a)/(1+2a) ,$$ (19)

a local maximum R_k^{11} is located at the point $x_{N-k} = 0$, $y_{N-k} = 0$. At the points (a,u) lying between curves $u_0(a)$ and $u = 1-a$, this maximum is located in the positive quadrant $(x_{N-k} > 0, y_{N-k} > 0)$; at the points (a,u) lying above $u_0(a)$, it is located in quadrant $(x_{N-k} < 0, y_{N-k} > 1)$.

It is not difficult to show that the problem of comparing R_k^{00} with R_k^{11} in the domain lying below $u_0(a)$ amounts to defining the sign of the expression

$$A(a,u) = -\frac{1-u^k}{1-u} [q(a,u) - u] - 1 ,$$ (20)

where

$$q(a,u) = u(1+a) + \frac{(1+a-u-2au)^2}{4a(1-u)} .$$

Negative values $A_k < 0$ correspond to $R_k^{11} < R_K^{00}$ and vice versa. Curves $u_k^2(a)$ obtained from $A_k(a,u) = 0$ are shown in fig.2.

The optimal development strategies constructed with the help of bifurcation curves (18) - (20) are the following (see fig.2).

1. In domain w_{00} bounded with segments of curves $u_{N-1}^1(a)$ and $u_{n-1}^2(a)$, the individual realizes a suboptimal strategy

$$(x,y)^1 = \cdots = (x,y)^N = 0; \; z^1 = \cdots = z^N = 1 ,$$ (21)

with the corresponding value of functional (15)

$$R_1^{\max} = am_1 \frac{1-u^N}{1-u} .$$ (22)

2. In the system of domains w_{1k} bounded with segments of curves $u_k^1(a)$, $u_{k-1}^1(a)$ and $u_0(a)$, an individual realizes strategies
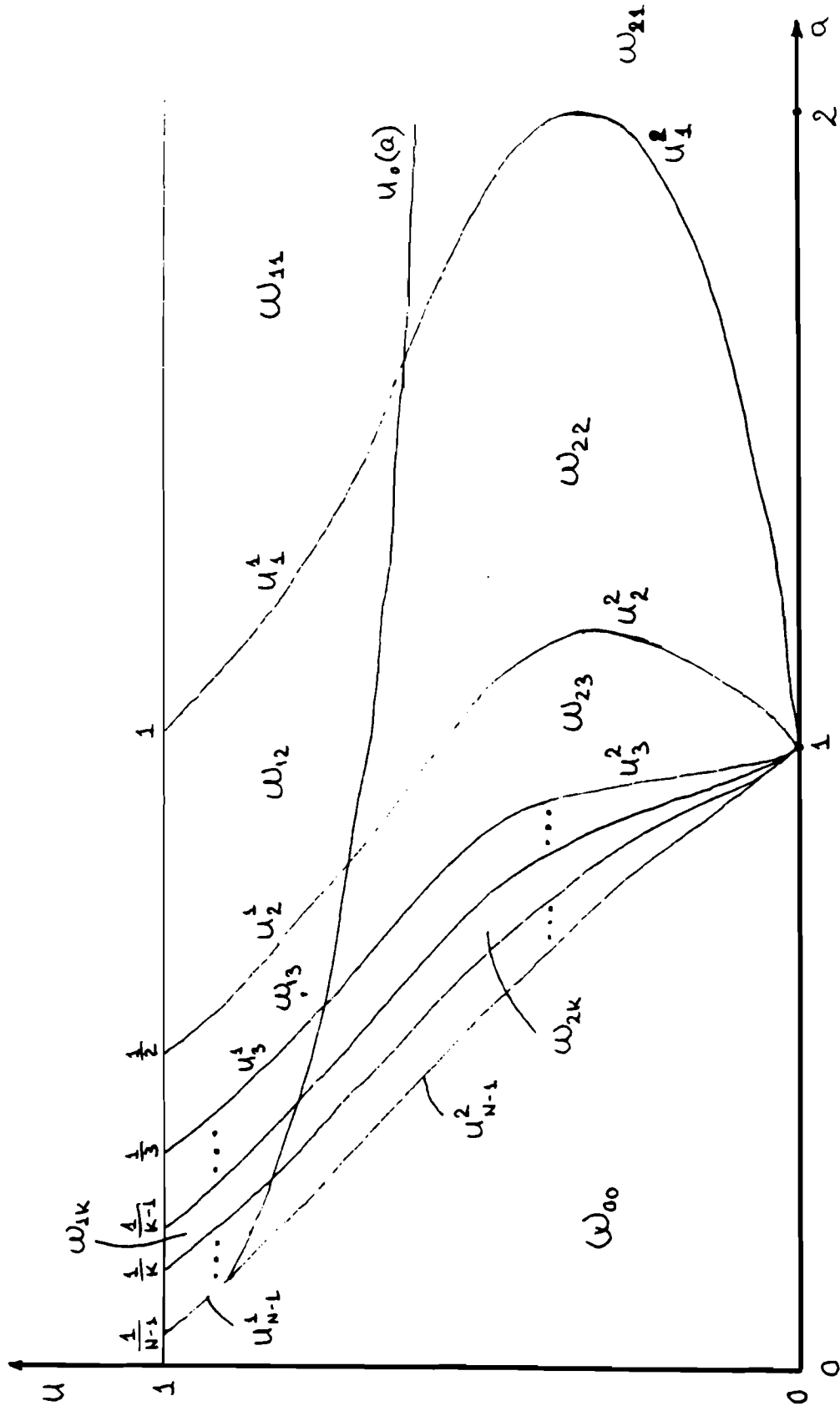
$$x^1 = \cdots = x^N = 0 ;$$

Figure 2: Separation of parameter's plane (a, u) for model (13-(15) into domains w_{jl} with different development strategies. For equations of bifurcation curves and optimal strategies, see text.

$$y^1 = \cdots = y^{N-k} = 1, \; y^{N-k+1} = \cdots = y^N = 0 \; ,$$

$$z^1 = \cdots = z^{N-k} = 0 \; , \; z^{N-k+1} = \cdots = z^N = 1 \; ,$$

with corresponding values of functional (15)

$$R_2^{\max} = am_1[u(1+a)]^{N-k} \; \frac{1-u^k}{1-u} \; . \tag{24}$$

Strategies obtained in a "growth-reproduction" model (Semevski, Semyonov, 1982) correspond to the case $u = 1$.

3. In the system of domains w_{2k} bounded with segments of curves $u_k^2(a)$, $u_{k-1}^2(a)$ and $u_0(a)$, an individual realizes strategies

$$x^1 = \cdots x^{N-k} = x^{\max} , \quad x^N - k + 1 = \cdots = x^N = 0 \; ;$$

$$y^1 = \cdots = y^{N-k} = y^{\max} , \quad y^{N-k+1} = \cdots = y^N = 0 \; ; \tag{25}$$

$$z^1 = \cdots = z^{N-k} = 0 \; , \; z^{N-k+1} = \cdots z^N = 1$$

where

$$x^{\max} + y^{\max} = 1 \; \text{and} \; x^{\max} = \frac{1+a-u-2au}{2a(1-u)}$$

Corresponding values of functional (15) are equal to

$$R_3^{\max} = am_1[q(a,u)]^{N-k} \; \frac{1-u^k}{1-u} \tag{26}$$

So all reproductive strategies are stepped, i.e., $z^i = 0$ is changed immediately by $z^{i+1} = 1$ (except for the suboptimal strategy (21)). Growth is always exponential with either $y = 1$ or $y = y_{\max} < 1$; dynamics of density is either exponential (strategies (21, (23)) with $n_{i+1} = un_i$ or "biexponential" (strategies (25)) with

$$n_{i+1} = [u + (1-a)x^{\max}]n_i \; , \quad i \leq N - k \; ;$$

$$n_{i+1} = un_i \; , \quad i > N - k \; .$$

The development strategies we obtained are clear from a qualitative viewpoint. At large values of u (system of domains w_{1k}) an individual grows during some part of its life and reproduces during the remainder, its defence expenses being equal to zero. The most appropriate domain is w_{11}, where an individual grows during the first $N-1$ steps and then reproduces at the Nth one. For a smaller u (systems of domains w_{2k}) an individual is required to expend resources on defence and on growth during the early part of its life before starting to reproduce. In conditions of resource deficiency (small a) and severity of site (small u) (domain w_{00}), an individual realizes a strategy of an "ephemeral" type, i.e., it

starts to reproduce only in the first step.

Thus the model (13)-(15) in spite of its simplicity describes plausibly the adaptation of optimal development strategies to different ecological conditions.

Optimal strategies in the model with competition (10)-(12) were investigated with the use of computer simulation. In contrast to the linear model (13)-(15), two new parameters appear, namely, intensity of competition l and initial density n_1. However, scale substitution $ln_i = s_i$ removes dependence on l and we have a right to vary, for example, l, with n_1 being constant. The simulations were made for $n_1 = 10^4$ and $N=10$; just as in the linear case, a search for the strategies was made on the parameters' plane (a,u) for the following set of values of l: $l = 10^{-4}$, 3.16 $\cdot 10^{-4}$, 10^{-3}, $3.16 \cdot 10^{-3}$ (these values were taken from a model (Korzukhin et al., 1987) that had been verified by field data on birch-siberian pine succession; in that model, the same expression was used for describing light competition).

The main effect found in model (10)-(12) consists of the presence of "smooth" reproductive strategies in contrast to stepped strategies of a linear model. The general pattern of behavior is the following: strategies z^k cease to be stepped with increasing $a, u, 1$, however, at the same time, there is an increase in the number of steps with $z^k \neq 0,1$. This pattern is found only when the value of u is big enough and all x^k are equal to zero. Thus the following strategy is added to strategies of the linear model:

$$x^1 = \cdots x^N = 0 ;$$

$$y^1 = \cdots = y^i = 1 ; y^{i+1},...,y^j \neq 0 ; y^j+1 = \cdots + y^N = 0 ; \qquad (27)$$

$$z^1 = \cdots = z^i = 0 ; z^{i+1},...,z^j \neq 0 ; z^{j+1} = \cdots = z^N = 0 .$$

An example of this strategy is shown in fig.3a; the corresponding dynamics of an individual's biomass and fertility are shown in fig.3b. The behaviour of population variables M and Q is qualitatively similar to that shown on fig.1.

Finally it is necessary to mention one more effect derived from the model. It is customary to suppose (e.g., see Bugrovski et al., 1982) that an individual gets its maximum biomass through the fact that respiration expenses increase faster than the rate of photosynthesis F; as soon as these quantities become equal, growth ends. According to development strategies obtained from the model, an increase in biomass ends because the individual begins to spend all photosynthetic products on seed production. It seems that both things take place in real life, i.e., there are both an increase of reproduction expenses and nonproportional (relative to biomass of leaves) growth of organs, that do not produce but consume photosynthetic products.
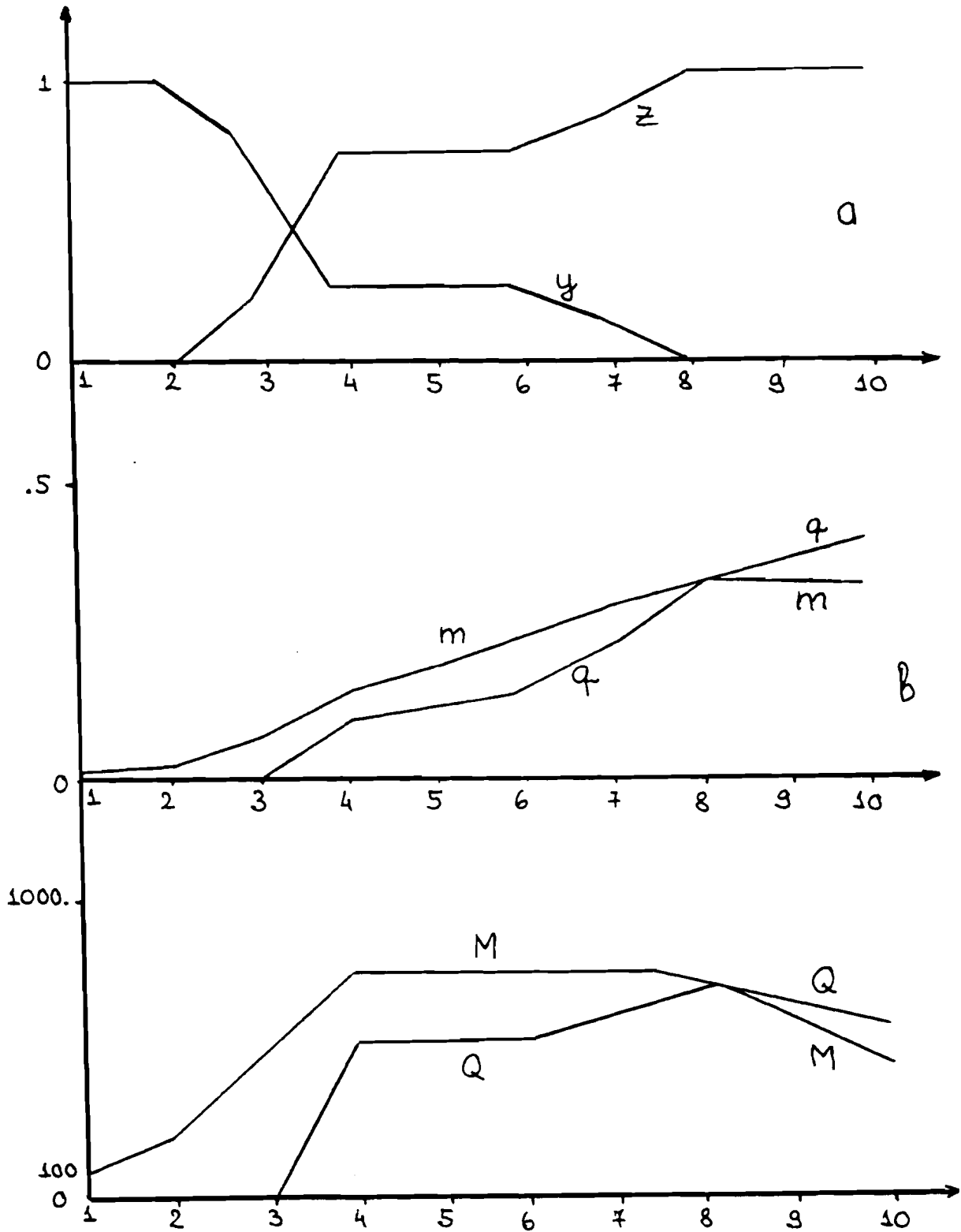
Figure 3   Solution of model (10)-(12) (obtained by means of computer simulation) for following values of parameters: $u = 0.08$, $a - 1.0$, $1 = 10^{-3}$, $n_1 = 10^4$, $N = 10$. Designations correspond to those used in (10-(12) and in legend to fig.1. Through z^k being identical to zero, the dynamics of population density is exponential and therefore is omitted.

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