POPULATION LEVEL MODELS OF FOREST DYNAMICS

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FOREWORD

This paper will also appear as a chapter in the book *Ecosystems Analysis and Simulation of the Global Boreal Forest*, edited by Professor H.H. Shugart, and to be published by Cambridge University Press. The scientific collaboration of Professors H.H. Shugart and M.Ya. Antonovski started in spring 1984 at Stockholm University. Their joint activities are reflected, for example, in writing two chapters for the book SCOPE–29, *The Greenhouse Effect, Climatic Change and Ecosystems*, edited by B. Bolin et al. In the following, the authors were collaborating with Professor Shugart within the Environment Program of IIASA.

Based upon a mathematical (analytical as well as an algorithmic) description, this paper is a serious attempt at a comprehensive assessment of forest dynamics and underlying processes. The results of this assessment could probably be used in the Boreal Forest Study of the Biosphere Dynamics Project.

Bo R. Döös, Leader
Environment Program

ABSTRACT

This paper outlines several general aspects of modeling forest dynamics. First we describe forest dynamics at the population level, based upon the results of certain dynamical equations. Second we consider above-ground plant species such as grasses and mosses, which are most important for boreal forests since they provide the boundary conditions for tree generations. Modeling creativity in this field is very limited, compared with tree systems, and is in reality more an art than science in view of its specific nature. Several examples in this direction are shown.

CONTENTS

POPULATION LEVEL MODELS OF FOREST DYNAMICS

M.D. Korzukhin and M.Ya. Antonovski***

1. INTRODUCTION

It is a long-standing tradition in mathematical ecology to use difference or differential equations in the modeling of forest dynamics at the population level. These dynamical equations are intended to describe the ecological mechanisms which determine the observed dynamics of a forest system, and do not include formalized descriptions such as regression formulae which feature widely in the forest modeling literature.

It is interesting to note that Newton's famous principle "It is useful to solve differential equations" has not been appreciated in the context of forest dynamics modeling. The current passion for an individual-tree approach in forest population modeling has meant that there has been interest in developing a dynamical equation technique. However, we believe that this classical approach (which is the single possible answer to the individual-tree approach) is complementary to the individual-tree approach; each approach allows the other to be used to its full potential.

There are some fields of forest dynamics where dynamical equations are indispensable. For example, the dynamics of grass and moss populations as part of the forest ecosystem cannot really be described at the individual-plant level; the same is true for all nonliving components of forest ecosystems such as dead organic material, nutrients, etc. In many other fields, dynamical equations need not be used but may be appropriate and useful. For example, the inevitable stochastic element in population dynamics when an individual-tree approach is used leads to difficulties in parameter estimation - the majority of calculative methods demand determination of parameter derivatives that are almost impossible in a stochastic system or can be only achieved with low accuracy. Dynamical equations, however, are ideally adapted for the calculation of the small trajectory modifications under small parameter variations that are needed for finding the derivatives.

It is clear from these general modeling considerations that this technique can be most successfully applied for comparatively simple population systems. The technique results in numerical solving, effective parameter estimation and - the most attractive theoretical aim - possible analytical results. Further, many boreal forest ecosystems are composed of a small number of tree and above-ground plant species, so the use of dynamical equations in this context can be of applied interest. In contrast, dynamical models for multi-species tropical and deciduous forests consist of many equations and parameters, so the deterministic behavior of tree number trajectories becomes so complex that it is near-stochastic. As a result, the advantages of a simple description by means of a dynamical equation technique over an individual-tree approach cease to exist.

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2. MAJOR DIVISIONS OF FOREST MODELING

The problems of the formulation of adequate forest models are in principle similar for individual-tree and dynamical equation techniques. In order to construct any model of a stand, one should describe, for multi-aged populations, 1) the free growth of one tree; 2) the mechanism of competition between trees; 3) the dependence of the viability of one tree upon available resources and environmental factors; and 4) conditions necessary for seed viability. Of these points, 1) and 2) are commonly required for individual-tree and dynamical equation techniques; 3) and 4) can be embodied in either deterministic or stochastic forms, thus giving two discussed approaches to forest modeling.

Given these major divisions, in various forms and details, the modeler should be able, in principle, to pick out a model with desirable properties. However, at present, we are some way from this ideal situation; there are still relatively few basic models and these have not been sufficiently tested to allow them to be used in such a way.

2.1. Tree Growth

The most physiologically correct and apparently most widespread approach to deriving tree growth equations involves the use of the concept of carbon balance (Davidson and Philip 1958, Richards 1959, Pienaar and Turnbull 1973, Aikman and Watkinson 1980, Bichele et al. 1980, Jarvis et al. 1981, Mäkelä 1986, and *multi alia*):

$$\dot{m} = S_L(m) \cdot A(R) - \mathrm{Re}(m) - U(m) \ . \tag{2.1}$$

In this equation, S_L is total leaf area, A – specific assimilation rate, R – resources of photosynthesis, Re – respiration, and U – decay losses.

In spite of the obviousness of (2.1), it is useful to note that when we consider long-term (e.g., one year) carbon balance, the difference $A - \mathrm{Re}$ cannot be less than zero. In fact, the balancing of (2.1) does not really represent the balance of tree biomass, but the balance of tree free assimilates (plus decay): free assimilates $= A - \mathrm{Re}$ when $A > \mathrm{Re}$ and $= 0$ when $A < \mathrm{Re}$.

Note that (2.1) uses only one variable (m) for the growth description of a whole tree, S_L, Re and U are expressed as functions of m. It is common for more than one variable to be introduced (Agren and Axellson 1980, Kull and Kull 1984, Oja 1985, Mäkelä 1988, etc.). In such cases, the authors are immediately confronted with the problem of assimilates distribution. Empirical difficulties are obvious, but theoretical approaches, which should be based on the optimization theory of growth, have not been satisfactorily developed.

In this area, the work by Rachko (1979), is of particular vote. In this work, the roots, stem and leaves of a tree are treated as independent variables, and the tree is assumed to be growing with the requirement of maximization of biomass increment during one year. The resulting description of photosynthesis is fairly realistic. Among recent works, we can mention Mäkelä (1988) who considered optimal tree height growth, and Korzukhin (1985) who introduced competition into the optimal growth task. The work by Korzukhin and Ter-Mikaelian (1987), who included tree defense, is discussed in Section 2.2.

Thus, we believe that a growth model description should take a form of a one-variable growth curve (e.g., $D(t)$–diameter or $m(t)$), and we recommend the use of the approach shown in (2.1) for this purpose.

Models differ in the forms of $A = A(R)$, $\mathrm{Re} = Re(m)$ and $U = U(m)$. Here we shall not consider the vast literature on corresponding models, but note only that the simplest and most widespread is the hyperbolic function $A(I)$, where $I = R$ is intensity of light. However, one needs to take care in the application of this classical light curve to a whole tree growing over a long period: the mechanism of photosynthetic adaptation can make function $A(I)$ almost linear (Tcelniker 1978). Respiration of growth is proportional to $S_L A$ and can be taken into consideration by a coefficient before member $S_L A$ in (2.1). In the simplest case, other components of respiration are taken to be proportional to m^δ (Bertalanffy 1957, Richards 1959, Pienaar and Turnbull 1973, Aikman and Watkinson 1980, etc.). In more complex cases, some elements of the respiration structure are introduced (Bichele et al. 1980, Mäkelä 1986). $U(m)$ is usually taken as being proportional to m.

Some authors (Botkin et al. 1972, Reed 1980, Shugart 1984, etc.) have used a semi-empirical analogue of the balance equation (2.1):

$$\dot{m} = S_L A (1 - m/m^{\max}) \ . \tag{2.2}$$

Due to (2.1) the value of $m^{\max}$ - maximum tree biomass (the root of $\dot{m} = S_L(m)\ A(R) - Re(m) - U(m) = 0$) depends on the assimilation rate A. For example, A and $m^{\max}$ are less in poor conditions. On the other hand, due to (2.2), $m^{\max}$ is independent of A, only the growth rate depends on A.

2.2. Tree Viability

This topic has not been as well developed as that of the description of tree growth. Formally, the problem consists a) of defining the concrete form of function

$$V(z) \tag{2.3}$$

- probability of survival of one tree over, one supposes, one year, and b) of defining the list of arguments, z, of this function, where z represents a number of variables describing the state of a tree or a population. These problems have not yet been fully investigated, so a certain degree of empiricism is present in all models of tree viability.

Several attempts have been made to establish the form of V on the basis of experimental data. In most cases, arguments of V used have been dimensional characteristics of the tree, its growth rate, and a parameter describing the pressure of competition. The dependence of V on these arguments is usually quite marked (*Figure 1a*) (Moser 1972, Monserud 1976, Glover and Hool 1979, Hamilton 1980, Buchman et al. 1983, Blagovidov 1984). Hamilton, Glover and Hool, and Buchman et al. used the exponential function

$$V = 1/[1+e^{-\varphi(z)}]$$

where z is a set of arguments, different for each of the cited papers ($z = D$, $z = G$, $z = \dot{D}, D/D$, competition index) and φ a linear growth function; here and below $G = \pi D^2 N/4$ is the stand cross-sectional area. Moser (1972) found from empirical observations that $V \approx 1 - e^{-aD}$. For a description of empirical data, Mitchell (1969) used the argument $z = S_c/S_c^m$ where S_c is the real crown projection and S_c^m the same for a free-growing tree. This argument means that a suppressed tree remembers its possible size if its growth is no longer suppressed. The same effect is proposed by Ek and Monserud (1974).

So far, the most profound approach to the problem has been the theoretical construction of Korzukhin and Ter-Mikaelian (1987) (see also Antonovski et al. 1987). Tree life function 'viability' is considered as being one of all other activities (growth and proliferation in these models). The tree is assumed to be a system which distributes its resources (free assimilates in these models) among the activities, and of high priority is the maximization total seed production. This is proportional to accumulated leaf area and life longevity, which in turn is determined by the amount of assimilates directed to defense. This distribution task was formalized and its solution showed that the share of assimilates directed to defense decreases monotonically with age. Also, a trajectory of optimal growth $m(t)$ and realistic age behavior of seed production was obtained; this was equal to zero until a certain age and thereafter increased monotonically in some cases, eventually stabilizing. The results of such an analysis for a free-growing tree and for a population of even-aged trees were qualitatively close. Despite being sound from the biological point of view, this approach does not lend itself to practical applications.

More practical modeling realizations of empirical observations can be divided into discrete and smooth, the first type being appropriate to individual-tree level models and the second to all kinds of models. The preferred argument of V is usually $\dot{D}$ because of its relatively easy field measurement.

The application of a step-line function V was initiated by Newnham and Smith (1964) who used $V = 1$ when $\dot{D} >$ const and $V = 0$ otherwise. This was used by Aikman and Watkinson (1980) taking S_L instead of $\dot{D}$. Mäkelä and Hari (1986) took $V = 1$ when $\dot{S}_L > 0$ and $V = 1 - \mid \text{const}\ \dot{S}_L/S_L \mid$ otherwise. In gap-modeling technique (Botkin et al. 1972, Shugart 1984, and *multi alia*) $V = 10^{-2/T}$ when $\dot{D} > 1$ mm/yr and $V = 10^{-0.2}$ otherwise, T is the life span of the species. Mitchell (1975) has taken $V = 1$ when $NH^2 <$ const and $V =$ value sustaining NH^2 otherwise.

The smoothed forms of V are also varied and, in addition, are more suited to an empirical approach. Korzukhin et al. (1987, 1988) applied

$$V = (R_I/R_I^{\max})^{\varphi} \tag{2.4}$$

where R_I is the light available for a tree, and a very similar argument was used by Mitchell (1969) (cited above). Zemlis and Shvirta (1987) took $V \approx GN$, and Cherkashin (1980) took $V \approx z^{\alpha} \exp(-1/z)$, $z = \dot{D}/D$. In their multi-aged population-level model (see Section 4.3.), Antonovski et al. (1989a,b) used $V = 1 - \text{const} \cdot (1-z)^{\beta}$, where $z = A/A_{\max}$ is the relative photosynthetic rate of a tree (*Figure 1b*). Pukkala (1987) applied $V \approx 1 - G/t$ as seedling viability. The first case of a smooth viability curve $V(\dot{D})$ in gap modeling was presented by Leemans and Prentice (1989).

To conclude this short review, we note that the way forward as far as definition of viability is concerned must lie in the use of evolutionary optimization principles (Pianka 1978, Semevsky and Semenov 1982). As yet, their application has not led to algorithms for the definition of V which are simple and reliable enough to be used in a forest dynamics model (see Korzukhin and Ter-Mikaelian 1987, and Antonovski et al. 1987).

2.3. Competition

Combined resources utilization leads to interaction between trees and unifies individuals in a stand, so competition can be considered as one of the two central phenomena which determine the dynamical behavior of a forest (the other is interaction connected with reproduction).

In essence, the problem consists of defining tree density dependence of two functions - assimilation rate in (2.1), $A = A[R(N)]$, and viability (2.3), $V = V[z(N)]$. Density can be the average number of trees per unit area, in populational-level and local approaches, or several neighboring trees around the central tree in the individual-level approach.

As in the cases of tree growth and viability, there are two ways of introducing density, namely formal and mechanistic approaches. The first is widely represented in forestry modeling and involves the formal introduction of "indexes" of competition, CI. When the individual-tree level is considered, CI are artificial functions of diameter, height, cross-sectional area, and biomass increments of neighbors of the tree in question (Mitchell 1969, Ek and Monserud 1974, Newnham and Smith 1964, Diggle 1976, Britton 1982, Smith and Bell 1983, Cennel et al. 1984, Ford 1975) or of local density, that is, number of trees (Plotnikov 1979), or of quite formal parameters of the central tree or its neighbors (Laessle 1965, *Growth Models ...* 1974, Lorimer 1983). When CI have been chosen, the correlation between the diameter increment of the central tree and CI is usually calculated, with the aim of testing the competition model.

When description is at the populational level, that is dynamical equations are used, CI are some function of mean population variables such as $\dot{D}/D$ (Cherkashin 1980), GN (Zemlis and Shvirta 1987), H^2N (Mitchell 1975), or N (Chjan and Chjao 1985).

The above approach is rather formal, in particular, CI may be used as an argument of A in (2.1) if one wants to interpret A in physiological terms.

The other, mechanistic, approach deals with the physical resources, R, available to a tree and tries to calculate their dependence upon density (taken again in two senses), that is to define the form of function

$$R(N,r) \ ,$$

where r are some dimensional characteristics of neighboring trees, or trees of the whole population. From general considerations it is clear that the results will depend on the type of resource, tree morphology and spatial pattern of the trees.

Our understanding of competition for light is considerably greater than that for soil resources. Usually, a uniform distribution of tree foliage is assumed (representation of producing layer) that immediately leads to the application of the Lambert–Beer penetration law (Botkin et al. 1972, plus all gap-modelers, Ross 1975, Mäkelä and Hari 1986, Oker-Blöm 1986, etc.). This law states that the amount of light at high level h can be given by

$$R_I(h) = R_{IO}\, e^{-\gamma\sigma^+(h)} \tag{2.6}$$

where γ is the extinction coefficient after transmission through one leaf layer which can depend on h, $\sigma^+(h)$ denotes the amount of foliage layer above level h, and R_{IO} is the initial light flux.

However, *sancta simplicita* of formula (2.6) is lost after the first refinement of the uniform model. Foliage in a stand is organized in tree crowns. Let us consider the question of light available to an average tree in a large population (Korzukhin and Ter-Mikaelian 1982). Each tree has a horizontal monolayer crown with area S_L, and $n(h)$ is the number of trees with height h. It is important that stem bases are distributed randomly over the plane, a requirement of Poisson's law. The extinction coefficient after one foliage screen transmission is equal to γ. By means of a geometrical probabilities technique, it was shown that under these conditions the classical formula (2.6) is true, where $\sigma^+(h) = \int_h^\infty S_L n(z)\, dz$. But a refusal of Poisson's distribution violates (2.6), this law is necessary for the fulfillment of (2.6).

Another example is provided by the same system but with, say, two-layered crowns. Each layer is close enough to the other to avoid intersections with other crowns and has area S, so $S_L = 2S$. Thus, the whole-tree absorption coefficient becomes equal to $\Gamma = 1 - (1-\gamma)^2$. Following our approach, $R_I(h)$ is given again by (2.6) but in the form

$$R_I(h) = R_{IO}\, e^{-\Gamma\sigma^+_{pr}(h)} \ ,$$

where σ^+_{pr} is the area of crown projections above level h, which in our case consists of 1/2 from $\sigma^+(h)$. Finally, we obtain

$$R_I(h) = R_{IO}\, e^{-\frac{\Gamma}{2}\sigma^+(h)} \ ,$$

that is the analogue of (2.6) with effective extinction coefficient $\gamma' = \frac{1}{2}[1 - (1-\gamma)^2]$ – a new violation of the uniform distribution model. Obviously k-layered crowns will give $\gamma' = \frac{1}{k}[1 - (1-\gamma)^k]$. The physical reason for this violation is clear: being organized in crowns, foliage screens have lost their freedom to move independently of each other, and only the whole crown (k screens together) has reserved this ability.

Several such grouping foliage models have been developed for crowns and stands (for review and references see Oker-Blöm 1986). If the possibility of crown intersections is to be taken into account, the analytical calculation of $R_I(h)$ is almost impossible.

Although root competition is equally as important in forest dynamics as competition for light, no one model has been developed that corresponds to that for light.

Most approaches do not use soil resources as explicit variables although some do – e.g., Alexandrov et al. 1986. Authors determine some 'qualitatively true' functions of total biomasses of competing trees (moss and grass if needed) – $G(M)$; it is usually assumed that root competition has a suppressive effect, so $dG/dM < 0$. These functions are then used as multipliers to assimilation rate function A, e.g., McMurtrie and Wolf (1983) and all gap-modelers. The most recent example of this (Shugart 1984) is multiplier for individual tree growth equation

$$B(M) = 1 - M/M^{\max} \ ,$$

where $M^{\max}$ is determined from field observations.

We can offer here a more realistic approach to the modeling of root competition, based once again on geometrical probabilities (Korzukhin 1986). Let us consider a population of identical screens, each having a thin, plane root system with area w. All are disposed at one level as is often the case for the boreal forest zone, so the process of competition is two-dimensional. Root systems are distributed according to Poisson's law over the plane, and from a unit area of the medium an amount E_o of resources (water, oxygen, etc.) is available. These resources are divided equally among all root systems which overlap at a given point; that is, from area w_1, which is not overlapped by other roots, the tree has amount $E_1 = w_1 \cdot E_o$ of resources, from area w_2, which is overlapped by one neighbor, it has $E_2 = \frac{1}{2} w_2 E$, etc. So, the total resources available to a tree are

$$E = \sum_{i=1}^{\infty} \frac{1}{i} \, w_i \, E_o \ , \qquad \Sigma \, w_i = w \ .$$

We are interested in the average amount of resources,

$$\bar{E} = \sum_{i=1}^{\infty} \frac{1}{i} \, \bar{w}_i \, E_o$$

where $\bar{w}_i$ are average areas of i-th overlapping. It can be shown that under Poisson's law $\bar{w}_i / w = \lambda^{i-1} e^{-\lambda} / (i-1)!$, where $\lambda = wN$ – average coverage of a unit area. Finally we have

$$\bar{E} = \frac{E_o}{N} \, (1 - e^{-wN}) \tag{2.7}$$

or

$$\bar{e} = \frac{E_o}{wN} \, (1 - e^{-wN}) \tag{2.8}$$

for the average specific resources $\bar{e}$ per unit area of root system. Whereas w was equal to the exploitation area of the tree, one can introduce the surface area of roots $\nu = q \cdot w$ (q – empirical coefficient), and use ν in (2.8). Magnitude $\bar{e}$ can now be used as an argument in the assimilation rate function, together with light, $A = A(R_I, \bar{e})$. One variant of this function was developed in Gurtzev and Korzukhin (1988) and applied in an individual-tree model of a linear pine stand; it was shown that taking into account the process of root competition improved appreciably the quality of growth description.

3. EVEN-AGED MONOSPECIFIC STANDS

3.1. Introduction

If, initially, we do not take into consideration the problems connected with the migration and establishment of seeds, even-aged stand modeling consists of the same basic elements as modeling of multi-aged and multi-specific stands. In both cases one must be able to formalize processes of competition, of individual tree growth (including, perhaps, changes in morphology) and of tree mortality. However, the field data relating to even-aged stands are much more accurate and numerous than those for multi-aged ones.

So it seems reasonable to adjust a population-level model on the basis of even-aged behavior first of all, and if this is successful, progress to the multi-aged behavior. Surprisingly, this apparently obvious way of model development has not been accomplished until now; even- and multi-aged stand models have developed independently.

3.2. Empirical Behavior of Even-Aged Stands

The required data can be taken from numerous observations at permanent plots. We shall restrict ourselves to the level of description of a stand which uses only the average characteristics of a tree, but not tree distributions. In this case, the system is described by the following variables: tree biomass m, diameter D, height H, leaf area S_L, and seed production p (per year). The population variables are: tree number N (per hectare), total biomass $M = mN$, leaf area $\sigma = S_L N$ (or close to σ cross-sectional area $G = N\pi D^2/4$), and total seed production $P = pN$.

For the purposes of model development it is necessary to know the behavior of these variables under variation of initial density $N(o)$ and ecological (site quality) parameters φ.

Time behavior. Individual tree variables have a simple form of monotonous sigmoidal functions; population variables (except N) are nonmonotonous and go through a maximum (*Figure 2*). After crown closure, a specific system invariant arises, connected with the maximum amount of leaves, $\sigma^{\max}$, which can be achieved in given ecological conditions

$$\sigma(t) = S_L(t)\ N(t) \simeq \sigma^{\max} \ . \tag{3.1}$$

Density behavior. Individual tree variables m, p and $D[t,N(o)]$ taken at any given moment decrease monotonously with the increase in initial density $N(o)$ (although $H[t,N(o)]$ is sometimes not monotonous). Maximum differences are observed somewhere in the middle of the set of trajectories for m (*Figure 3*).

If one considers tree number dynamics under various $N(o)$, one can observe the effect of 'forgetting' of initial conditions (*Figure 3*), that is $N[t,N_2(o)]/N[t,N_1(o)] \longrightarrow 1$ for all $N_{1,2}(o)$. This 'drawing-together' effect means that tree mortality depends upon density (and increases as density goes up).

Population variables M, G, P, and $\sigma[t,N(o)]$ increase at first with increased $N(o)$. Due to somewhat rare data (Hirano and Kira 1965, Buzykin 1970, Redko 1978) their maximum values $M^{\max}$, etc., begin to decrease under very large $N(o)$ (*Figure 4*). We call this effect 'overcrowding'. The time at which these variables reach their maximum values, $t_{M,G,\sigma}[N(o)]$, decreases with increasing $N(o)$ (*Figure 4*).

Site quality effects are obvious for individual trees. At the population level, tree numbers are smaller in the better site conditions (under the same initial conditions) (*Figure 5*). In spite of this effect, total biomass and other population variables increase.

Tolerance effects. Under the same initial conditions, tree numbers are greater for more shade-tolerant species (*Figure 5*).

3.3. Dynamical Models of Even-Aged Stands

Surprisingly, there are no even-aged stand models which are able to describe all properties of the system enumerated in Section 2.2.; there exist only some formalized constructions relating to different parts of the whole picture.

A number of works are traditionally devoted to tree number behavior only. Among them, there are linear equations $\dot{N} = -d(t)N$ where $d(t) = 1 - V(t)$ is mortality as given function of age (Hilmi 1957, Terskov and Terskova 1980, and others); obviously, this equation does not 'forget' initial conditions $N(o)$ and consequently cannot describe the 'drawing together' of trajectories. In addition, there are nonlinear 'Volterra-type' equations, e.g., $\dot{N} = -aN[(1-(b/N)^{\lambda}]$ (Chjan and Chjao 1985).

On the other side, there are 'productivity' models, operating with one variable M: $\dot{M} = aM^{\alpha} - bM$ (e.g., Pienaar and Turnbull 1973, Budyko 1977, and others); obviously, this equation cannot describe going $M(t)$ through its maximum.

The majority of modeling efforts in this area have been devoted to a special class of model based on different forms of the 3/2 law invariants (Reineke 1933, White and Harper 1970, Hozumi 1980, Lonsdale and Watkinson 1983, Zeide 1987, and *multi alia)*.

$$\mu = wN^{\alpha} = \text{const} , \tag{3.2}$$

where $w = S_L, m, D, H$. It is likely that the possible population-level 'invariant' is interrelation (3.1), so (3.2) is, in fact, (3.1) rewritten in terms of other variables.

If our aim is to model the whole scenario adduced in Section 3.2., interrelation (3.2) appears to be very restricted. Firstly, it cannot be related to the part of the trajectory $M(t)$ which lies behind $M^{\max}$. If we put $w = m$ (classical variant of Yoda et al. 1963), then $\mu = mN^{\alpha} = MN^{\alpha-1} = \text{const}$; because of $\dot{N} < 0$ this leads to $\dot{M} > 0$, because $(\alpha-1)$ is greater than 0, so that (3.2) can be true only before $M^{\max}$, where $\dot{M} = 0$. Secondly, it cannot take into consideration the important dependence of the trajectories on initial density $N(o)$, as this value is not 'remembered'.

The most developed approach of Hozumi (1980) uses, besides invariant (3.2), nonautonomous dynamical equations and looks artificial.

All types of dynamical analysis of even-aged stands based on the 3/2 law give us a 'semi-model', which is intended to substitute the formulation and analysis of a full nonlinear system of dynamical equations.

It seems to us that in this area there is a certain magic of simple formulae, and that researchers have now extracted from them all that is possible.

3.4. Base Model 1 of Even-Aged Stands

Below we use the simplest model elements of growth, viability and competition for the composition of even-aged model 1. The aim of this model is to describe the maximum dynamical properties of even-aged stands enumerated above.

1. Calculations using growth equation (2.1) for free-growing trees and trees experiencing competition show that it works well when

$$S_L(m) = am^{\alpha} \tag{3.3}$$

and when

$$\mathrm{Re}(m) + U(m) = cm \tag{3.4}$$

(see papers in Richards 1959, *Growth Models...* 1974, Gurtzev and Korzukhin 1988, etc.). Interrelation (3.3) can be derived from two well-established ties: $S_L \approx D^\beta$, $1.5 \leq \beta \leq 2$ (Mohler et al. 1978, Mäkelä 1986, etc.), and $m \simeq D^\delta$, $2.5 \leq \delta \leq 3$ (numerous yield tables). As a result we obtain (3.3) with $0.5 \leq \alpha \leq 0.8$.

2. It is appropriate to separate density-dependent and density-independent parts of full viability Y (Semevsky and Semevov 1982). Denoting the first as W and the second as V (as above – (2.3)), we have $Y = W \cdot V$. In the construction of V, we are working from the basis of the following propositions: (i) it should be based on a resources approach; arguments such as $\dot{D}$ are considered to be indirect reflexes of the real viability mechanism, which is in essence the use of tree resources for defense and repair; (ii) we will abandon the 'memory' arguments such as $m(t)/m^{\max}(t)$ for the sake of simplicity, since they demand a second growth variable (for $m^{\max}(t)$ in this example); (iii) because photosynthesis is the central process of tree resource production, we suppose that assimilation rate A should be the argument of V in (2.3)

$$z = A/A_{\max} \tag{3.5}$$

(normalized for suitability).

Following (2.1) and (2.5), A depends on N through R, that is $A = A[R(N,m)]$; when $N = 0$, $R = R^{\max}$, $A = A_{\max}$, $z = 1$, and $V = 1$, we obtain a free-growing tree.

Finally, we have base model 1 (specific death rate is equal to $1 - Y$):

$$\begin{cases} \dot{N} = -\{1 - W \cdot V[A(R(N,m))/A_{\max}]\}\, N \\ \\ \dot{m} = S_L(m)\, A[R(N,m)] - cm \quad , \end{cases} \tag{3.6}$$

where $S_L(m)$ is given by (3.3), $W \leq 1$, $V \leq 1$, A is given by any model of photosynthesis, and R is given by the model of competition.

Below we adduce a simplified analytical example of the use of (3.6). Again, we consider the competition for vertically directed light among populations of Poisson-law–distributed trees with horizontal crowns, thinly spread over height. This gives (Korzukhin and Ter-Mikaelian 1982)

$$R(N,m) = R_o \exp\,[-\frac{1}{2}\,\gamma\, S_L(m)\, N] \ . \tag{3.7}$$

Consider the situation when competitive interaction is weak, that is $x = \gamma\, S_L(m)\, N \ll 1$, and undertake Taylor's expansion of A near $x = 0$ and V near $z = 1$:

$$A(x) = A(o) - |\frac{dA}{dx}|\, x - \cdots \ ,$$

$$V(z) = V(1) - \frac{dV}{dz}\,(1-z) - \cdots \ ,$$

where $A(o) = A_{\max}$, $V(1) = 1$ and the argument of V is

$$z = A(x)/A_{\max} = 1 - \frac{1}{A_{\max}}\,|\frac{dA}{dx}|\, x - \cdots \ .$$

Assuming that all first derivatives are not equal to zero, $|\frac{dA}{dx}| = a_1 \neq 0$, $\frac{dV}{dz} = b_1 \neq 0$, we obtain a system of first approximation

$$\begin{cases} \dot{N} = - \{1 - W[1 - a_1 b_1 \dfrac{1}{A_{\max}} x]\} N \\[2ex] \dot{m} = S_L(m)\, A_{\max} [1 - \dfrac{a_1}{A_{\max}} x] - cm \ . \end{cases} \tag{3.8}$$

$$(x = \gamma\, S_L(m)\, N)$$

Now suppose that density-independent mortality is absent, $W \equiv 1$, respiration and decay losses in $\dot{m}$ are negligible, and $a_1 x / A_{\max} \ll 1$, that is growth is free. The result is an idealized system

$$\dot{N} = - p m^{\alpha} N^2 \ ; \quad \dot{m} = q m^{\alpha} \tag{3.9}$$

$(p = \alpha a_1 b_1 \gamma / A_{\max};\ q = a A_{\max})$ and its solution under initial conditions $N(o) = N_o$, $m(o) = m_o$:

$$m(t) = [(1-\alpha)\ qt + m_o^{1-\alpha}]^{1/1-\alpha} \tag{3.10a}$$

$$N(t) = \left\{ \frac{1}{N_o} - p\frac{m_o}{q} + \frac{p}{q}\ [(1-\alpha)\ qt + m_o^{1-\alpha}]^{1/1-\alpha} \right\}^{-1} \ . \tag{3.10b}$$

It is clear that solution (3.10a) quickly forgets initial condition m_o (weight of seed), so the formulae are simplified:

$$m(t) = [(1-\alpha)\ qt]^{1/1-\alpha} \ , \quad N(t) = \left\{ \frac{1}{N_o} + \frac{p}{q}[(1-\alpha)\ qt]^{1/1-\alpha} \right\}^{-1} \ . \tag{3.11}$$

We also need a generalized population variable of the form $F = m^{\beta} N$, which, from (3.11), is equal to

$$F(t) = \frac{r_1 t^{\beta/1-\alpha}}{1/N_o + r_2 t^{1/1-\alpha}}$$

$$(r_1 = [(1-\alpha)\ q]^{\beta/1-\alpha} \ , \quad r_2 = p(1-\alpha)^{1/1-\alpha} q^{\alpha/1-\alpha}) \tag{3.12}$$

F represents M, σ and G when β is taken as needed, and under $\beta < 1$ it goes through a maximum when $t = t_F^{\max}$:

$$F_{\max} = N_o^{1-\beta}\ A_{\max}^{2\beta}\ f_1(\xi) \ , \tag{3.13}$$

$$t_F^{\max} = \frac{1}{N_o^{1-\alpha}} \cdot \frac{1}{A_{\max}^{2\alpha-1}}\ f_2(\xi) \ , \tag{3.14}$$

where we have included in f_1 and f_2 all dependencies upon the rest of the parameters which are not of interest here.

Formulae (3.10)–(3.14) correctly describe many properties of even-aged system behavior.

1. From (3.10b) density $N[t, N(o)]$ forgets initial conditions $N(o)$ and converges to a 'magistral' trajectory (*Figure 3*):

$$N(t) = \frac{1}{a_1 b_1 \gamma a^{1/1-\alpha} A_{\max}^{2\alpha-1/1-\alpha}} \cdot \frac{1}{t^{1/1-\alpha}} \ . \tag{3.15}$$

2. When site conditions meliorate, $A_{\max}$ increases and $N(t)$ diminishes at any given t (*Figure 5*) if one supposes $\alpha > 0.5$ (a fairly realistic condition).

3. If we consider more shade-intolerant species, b_1 increases and $N(t)$ again diminishes (*Figure 5*).

4. When N_0 increases, $F_{\max}$ increases also (for $\beta < 1$) corresponding to the behavior of $\sigma^{\max}(N_0)$ and $G^{\max}(N_0)$ (*Figure 4*) under a relatively small N_0.

5. Magnitude $t_F^{\max}(N_0)$ (*Figure 4*) also decreases under better site conditions (when $\alpha > 0.5$).

Taking into account respiration and decay in the tree growth equation, $\dot{m} = qm^{\alpha} - cm$, will make $M(t)$ go through a maximum, $m(t)$ becomes finite but $N(t) \longrightarrow 0$, and addition of competition will obviously give a set of trajectories $m[t,N(o)]$.

Finally, the only dynamical effect which cannot be given by base model 1 (3.6) is the 'overcrowding' (*Figure 4*) under large $N(o)$; it can be shown that this effect demands at least three dynamical variables.

One can easily see that the form of system (3.8) and all results do not, in fact, depend necessarily on the resource under competition – they also depend on the soil resource. Bearing in mind the proposition about weak interaction, one can take Taylor's expansion of (2.8) and repeat the calculations with $x = qw(m)\ N \ll 1$.

The topic of numerical applications of system (3.6) is worthy of a separate paper. It seems to us that the above considerations show clearly the ability of base model 1 to be used for natural forest modeling.

4. MULTI-AGED STANDS

In the array of inevitably complicated elements in the field of forest dynamics, multi-aged monospecific stands are the simplest elements, ones which can be related to real natural forest. The only process which needs to be added here in comparison with an even-aged population is the origin of seedlings. This gives us a usual population demographical system with a complete collection of dynamical processes.

It is then necessary to undertake a model description of the combined dynamics of the set of age cohorts which represent the whole population. There are some variants of the mathematical embodiment of the dynamics of the population which are distinguished by age and consequently by tree size and we shall review them briefly.

4.1. Construction of Demographical Models

There are a number of similar ways to formalize a population's age dynamics. The first approach was illustrated in Von Foerster (1959) who considered $n(t,\tau)$ – quantity of individuals with given age τ at time t – and processes of birth and death, ignoring growth. This corresponds to the model

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial \tau} = -d(t,\tau)\ n \quad , \quad n(t,0) = \int B(t,z)\ n(t,z)\ dz \ . \tag{4.1}$$

Here d and B are specific death and birth rates; note that they are independent of population density n, that is the model is linear. This simple approach has now been exhausted from the mathematical point of view (Sinko and Streifer 1967, *Dynamical Theory of Biological Populations* 1974) and is of no interest for forest dynamics. Extensions of model (4.1) have been developed in various directions. Gurtin and MacCamy (1979) introduced density-dependent mortality $d = d(\tau,N)$ where $N = \int n d\tau$ and obtained analytical results for partial cases of $d(N)$. Sinko and Streifer (1967) considered a two-dimensional system, combined age and size distribution $n = n(t,\tau,m)$ where m is any quantitative characteristic of the individual. Behavior of n in the most general case is derived by the equation

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial \tau} + \frac{\partial}{\partial m} \left[g(t,\tau,m,n)\ n \right] = -d(t,\tau,m,n)\ n \tag{4.2}$$

with corresponding boundary conditions; here $g = \dot{m}$ is the growth rate of the organism. Competitive and other density-dependent aspects are taken into account by means of argument n in g and d. In this case, equation (4.2) is very complex for analytical consideration and Sinko and Streifer (1967) have examined a partial case when (4.2) is linear by n,m, that is $g = g(t,\tau)$, $d = d(t,\tau)$.

Another and more popular approach was proposed by Leslie (1945) whose wellknown matrix technique is the discrete analogue of the continuous-time model (4.1) and is more suitable for solving by computer. Leslie dealt with age distribution $n(t,\tau)$. It is convenient for us to write out his model in a 'cohort' form and with a generalized variant:

$$\begin{cases} n(t+1,\tau+1) = Y(t,\tau,<n>)\ n(t,\tau)\ , \quad \tau = 1,\ldots,T-1 \\ \\ n(t,1) = \Sigma\ B(t,\tau,<n>)\ n(t,\tau) \end{cases} \tag{4.3}$$

where t, τ are discrete, Y, B are viability and birth rate, and $<n>$ is a generalized vector argument, $<n> = n(t,1),n(t,2),\ldots,n(t,T)$ which describes density effects.

Leslie (1945) and many others have used this model with $Y,B = Y,\tau,B(\tau)$ only, that is the simplest linear variant which enables powerful matrix analysis. It is clear that in the case of forest dynamics this proposition is true either for low densities or for short time periods until argument $<n> \simeq$ const.

Among recent works we can note a two-species age-distributed model - an application of system (4.3), presented in Korzukhin et al. (1987, 1988). This was applied to 200-year post-fire successional dynamics in West Siberia. Growth curves for both species (birch and Siberian pine) were fixed, so only age number dynamics were analyzed, that is, behavior of magnitudes $n_1(t,\tau)$, $n_2(t,\tau)$. Crowns were horizontal and light competition interaction was directed from higher to lower trees only. The dynamics of two age packages ('waves') observed in the field (see also Section 4.2.) were described numerically.

In forest dynamics applications the Lefkovitch (1965) approach is more popular, which offered the same technique for size distribution analysis (sizes of trees are measured much more easily than their ages). If one breaks the size axis m into Q intervals

$$(\mu_o,\mu_1)\ (\mu_1,\mu_2) \cdots (\mu_{Q-1}\mu_Q) \tag{4.4}$$

and takes all trees whose sizes belong to interval i, that is $\mu_{i-1} \le m < \mu_i$, then the system dynamics will be represented by the following scheme:

$$\begin{tikzcd}
 & \text{death} & \text{death} & \\
\text{birth} \arrow[r] & n(t,1) \arrow[u, "d_1"] \arrow[d, "1-g_1-d_1"] \arrow[dr, "g_1"] & n(t,2) \arrow[u, "d_2"] \arrow[d, "1-g_2-d_2"] \arrow[dr, "g_2"] & \text{etc.} \\
\text{birth} \arrow[r] & n(t+1,1) & n(t+1,2) & {}
\end{tikzcd} \tag{4.5}$$

where $n(t,i)$ is tree number on i-th size interval, g_i is growth and d_i is death rate. It is proposed, for the sake of simplicity, that changes in sizes are small and occur only between neighboring classes. Dynamical equations, being discrete analogues of differential equation (4.2), are easily written from the balance scheme (4.5):

$$\begin{aligned} n(t+1,i) &= n(t,i) + g(t,i-1,<n>)\, n(t,i-1) \\ &\quad - g(t,i,<n>)\, n(t,i) - d(t,i,<n>)\, n(t,i) \\ n(t+1,1) &= n(t,1) + \sum_i B(t,i,<n>)\, n(t,i) - g(t,1,<n>)\, n(t,1) \\ &\quad - d(t,1,<n>)\, n(t,1) \qquad\qquad I = 2,\ldots,Q \end{aligned} \tag{4.6}$$

Here B is size-specific fecundity, argument $<n>$ is analogous to that used in (4.3), and dependence of g, d, B upon i means their dependence on size. In these equations, the magnitudes of size intervals $\Delta\mu_i$ are considered to be included in functions g, d, B.

The most frequently used variant of the highly generalized model (4.6) consists of taking birth, growth and death rates as depending only upon size (class number i). Buongiorno and Bruce (1980) have applied this model to the task of productivity maximization in a linear variant, when $g = g(i)$. Hartshorn (1975) has used this type of model for two tropical tree species, and Dyrenkov and Gorovaya (1980) for one spruce species. The value and restrictions of the linear approach were noted above. Kapur (1982) undertook an important extension of the task by introducing $g = g(N)$, that is, a rough description of density-dependent factors. The aim was again to maximize total stand productivity. A complex nonlinear model with $g,d,B = g,d,B(i,<n>)$ was formulated by Cherkashin (1980) and applied to the dynamics of a seven-species boreal forest in South Siberia.

A major weakness in the described matrix and time-continuous multi-aged models is the rather formal realization of individual tree growth and competition mechanisms. From this point of view, individual tree models are better developed.

A third way to describe age and size dynamics is by means of a combination of Leslie and Lefkovitch's matrix technique or by means of straight generalization of our even-aged model (4.6). This method was proposed and realized in Antonovski et al. (1989a,b). The central idea is simply to add an age cohort growth equation to the cohort number dynamics equation that doubles the number of variables and gives the model

$$\begin{cases} n(t+1,1) = \sum_\tau B(t,\tau,<n>,<m>)\, n(t,\tau) + f \\ n(t+1,\tau+1) = Y(t,\tau,<n>,<m>)\, n(t,\tau) \qquad \tau = 1,\ldots,T-1 \\ m(t+1,\tau+1) = m(t,\tau) + g(t,\tau,<n>,<m>) \end{cases} \tag{4.7}$$

with boundary conditions $m(t,1) = m_1$. Obviously, variable m can be substituted by arbitrary size characteristics of a tree. Argument $<m>$ has the same meaning as $<n>$. Note that Leslie's system (4.3) is the obvious partial case of (4.7). In order to obtain (4.3), one would simply not take into consideration all equations for $m(t,\tau)$, that is, to suppose that growth curve $m(\tau)$ is fixed and already given.

We have added one new element in model (4.7) compared with (4.3) and (4.6), namely addendum f in the equation for first age class. This element describes seed influx in the system due to the background of seed which usually exists in forested areas. This addition introduces a spatial aspect to the system analysis which is absent in the standard form of Leslie and Lefkovitch's models. Let us briefly discuss the comparative potential of size and age cohort approaches, that is, systems (4.6) and (4.7).

Major differences are the following. (4.7) is a purely deterministic system, giving one trajectory of biomass and tree number for a given cohort, so that an even-aged system at each time moment is described by only two magnitudes – $m(t+k,k)$ and $n(t+k,k)$; k is age of cohort born at moment t. In contrast, (4.6) describes spreading of sizes (and numbers, correspondingly) about the m–axis, even for one cohort. In reality, after k steps each cohort will be partially presented in all size classes from 1st to $(k+1)$st. So, certain stochastic mechanisms are contained in (4.6); in its strictest sense, as it deals with size distribution, it is analogous to a Markov chain.

The two systems also have similarities. Both give us size distribution – model (4.6) by the definition of $n(t,i)$ and model (4.7) after simple summation over given size interval (4.4):

$$n(t,i) = \sum_{\tau} n(t,\tau) \ , \tau_i \leq \tau < \tau_{i+1}$$

where τ_i, τ_{i+1} are the ages whose tree size m_i belongs to i-th interval, $\mu_i < m_i < \mu_{i+1}$. Both systems also give us age distribution – model (4.7) by the definition of $n(t,\tau)$ and model (4.6) by means of a principally clear but rather sophisticated procedure of watching the fate of each cohort which spreads in the set of size cohorts. Let us examine a simple example. Consider the fate of a cohort which was born at time t, with number of trees $n(t,1)$. At time $t+k$ there will be $n(t+k,k+1) = g_1,g_2,\ldots,g_k n(t,1)$ trees in size class $k+1$, $n(t+k,k) = g_1,g_2,\ldots,g_{k-1}(1 - g_k - d_k)\ n(t,1)$ trees in size class k, etc. Summing up all these numbers gives us the total number of trees of age $\tau = k$:

$$n(t+k,\tau) = \sum_{i} n(t+k,i) \quad .$$

It seems to us that (4.7) has some advantages over (4.6). For the latter, in the case of several species, a common set of size intervals (4.4) makes the species growth resolution different; a particular set makes the whole system almost inoperable (e.g., if we need, as is often the case, to compare species heights for defining competitive relations). This approach is disquieting when one has to deal with a number of tree species with noticeably different growth rates and, moreover, try to include a description of, say, grass and shrub growth. System (4.7) does not have any of these disadvantages. The size-classes approach can, of course, be useful for one-species even-aged tasks aimed at analyzing size distribution dynamics.

In conclusion, then, we can call (4.7) 'base model 2'. In the next section we will show its simulation abilities using an example of the modeling of nonstationary age distribution behavior.

4.2. Empirical Age Dynamics in Simple Forests

First of all, we will describe the situation of nonstationary age distribution behavior of a generalized coniferous species. Such a situation originates after a severe catastrophic disturbance which entirely obliterates the initial 'material' stand and provides zero initial conditions

$$n(t = o,\tau) \equiv 0 \quad . \tag{4.8}$$

This situation is typical of major fires in taiga forests, total phytophag defoliation (after which the trees quickly wilt and die), windfall of over-mature trees and, of course, cutting by man. The subsequent successions have been repeatedly described and analyzed in the literature (Semetchkin 1970, Leak 1975, Hett and Loucks 1976, Larson and Oliver 1979, Oliver 1981, etc.).

Further, the intensity of seed influx f will be the central ecological parameter. Clearly, at sufficiently low f values and over a long enough time period, the area will be inhabited by a population with a monotonous age distribution $\partial n/\partial\tau < 0$, which attains equilibrium during one generation time. This case is typical for habitats with poor soil and climatic conditions.

In comparatively better conditions, and when f is large enough, pioneer individuals capture the area and exhaust the resources (light, soil oxygen, nitrogen, etc.), and the seedlings of the next ages die off due to competitive suppression. The result is a 'package' of older trees and a zero-gap at that part of the age distribution which corresponds to younger trees (*Figure 6*), a picture that has been described repeatedly (Zubarev 1965, Semetchkin 1970, Kazimirov 1971, Leak 1975, Sprugel 1976, Francline and Waring 1979, Larson and Oliver 1979, Oliver 1978, 1981, Glebov and Kobyakov 1984. For a full review of different types of nonstationary age distributions, see Katayeva and Korzukhin (1987) and Antonovski et al. (1989c). In both cases we have the 'running wave' or several waves along τ–axis.

The subsequent dynamics may go one of two ways: a) after one or several damping waves the age distribution attains equilibrium; b) the system enters an oscillating regime which can be either fully or quasi-periodic. For a full review of field observations, see Antonovski et al. (1989a). Here we will list only some typical cases. A prolonged (100–200 years) endogenous periodic was reported for deciduous forests in the Far East (Kolesnikov 1956, Vasiliev and Kolesnikov 1962, Rozenberg et al. 1972), for fir forests in the Ural region, (Smolonogov 1970, etc.), for Beech Crimea forests (Sukachev and Poplavskaya 1927), and for Balsam Fir and Eastern Hemlock forests in the Great Lakes region (Hett and Loucks 1976). An endogenous periodic of 60–80 years was reported for *Abies* forests in New England (Sprugel 1976, Reiners and Lang 1979, Foster and Reiners 1983, Moloney 1986) and for *Abies* forests in Japan (Oshima et al. 1958).

Unfortunately, only several works (Hett and Loucks 1976, Reiners and Lang 1979) give information about age distributions. Of great importance are the data about the size of area which is occupied by a single-phase stand – this area is usually between 0.02 and 1 ha (Oshima et al. 1958, Foster and Reiners 1983, Moloney 1986).

A further set of works is dedicated to spatial waves in pure dark-coniferous stands (Oshima et al. 1958, Sprugel 1976, Reiners and Lang 1979, Foster and Reiners 1983, Moloney 1986). If the system is observed in a single 'point' – reported to be above 0.02–1 ha – it exhibits periodicity of age distributions of trees. Spatial waves are generated by synchronization of phases in different points owing to strong, undirected winds. When there are no winds the phases of development become different.

The next section is devoted to modeling analysis of periodic phenomena.

4.3. One-Species Oscillation Models

First, we offer two simplified qualitative models (for details see Korzukhin 1980, Antonovski et al. 1989a,b), which are some particular cases of the general multi-aged system (4.7).

A. The first system is differential and describes number dynamics in a system with three age classes.

$$\begin{cases} \dot{n}_1 = V(\gamma\sigma)\, f - n_1 \\ \dot{n}_2 = n_1 - n_2 \\ \dot{n}_3 = n_2 - n_3 \end{cases} \tag{4.9}$$

Here we ignore the mortality in class 2 and consider the seed background as the only source of regeneration – its intensity is f and offspring survival is V, depending on total leaf area, $\sigma = S_2 n_2 + S_3 n_3$ ($S_1 n_1$ is neglected) and γ is a generalized interaction, for example, coefficient for light absorption. By using trivial qualitative equilibrium point analysis, it is easy to show that system (4.9) can realize a sustainable oscillation. For example, when $V = \exp\,(-\,\gamma\sigma)$, this will happen when

$$f \geq \frac{8}{\gamma(S_3 - 2S_2)} \exp\,[8(S_2 + S_3)/(S_3 - 2S_2)] \ . \tag{4.10}$$

B. The discrete analogue of system (4.9)

$$\begin{cases} n_1(t+1) = V(\gamma\varphi)\,f \\ n_2(t+1) = n_1(t) \\ \dots\dots\dots\dots\dots\dots \\ n_T(t+1) = n_{T-1}(t) \end{cases} , \tag{4.11}$$

where $\sigma(t) = \Sigma\ S(i)\ n_i(t)$, with step-wise survivability function and linear law of growth

$$V(\gamma\sigma) = \begin{cases} 1 \text{ when } \sigma < \sigma* \\ \\ 0 \text{ otherwise} \end{cases} ; \quad S(i) = a(i-1)$$

realizes stable age oscillations. For example, when $af > \sigma*/(T-1)$, there is a regime with period

$$\theta = T + K \ ; \quad K = \left[\frac{\sqrt{8T-7+1}}{2}\right] \ ;$$

$[z]$ denotes integer part of z. The schematic solution of (4.11) with zero initial conditions has the form of a periodically running wave with K non-zero classes in a package:

$$\begin{aligned} n_i(t) = (0,\dots,) &\longrightarrow (f,0,\dots,0) \longrightarrow (f,f,0,\dots,0) \longrightarrow \\ &\longrightarrow (0,\dots,0\ \underbrace{f,\dots,f}_{K},\ 0,\dots,0) \longrightarrow \cdots \longrightarrow (0,\dots,0,f) \longrightarrow (0,\dots,0) \ . \end{aligned}$$

For numerous variations based around this approach, see Antonovski et al. (1989a,b).

The numerical and realistic oscillation model (Antonovski et al. 1989b) originates from the general form of base model 2 (4.7). Its concretization for our purposes uses simply the sum of one-cohort equations (3.6). Crowns morphology was the most simple – they were horizontal with areas

$$S_L(t,\tau) = am^{\alpha}(t,\tau) \tag{4.12}$$

(a,α – parameters); decay and respiration was given by (3.4). Assimilation was proportional to light flux

$$A[R] = bR(t,\tau) \ , \quad A[1] = A^{\max} = b \tag{4.13}$$

where R is given by

$$R(t,\tau) = R_o \sin\varphi \exp\,[-\ 1/2\ \gamma\ S_L(t,\tau)\ n(t,\tau) - \gamma \sum_{\mu=\tau+1}^{T} S_L(t,\tau)\ n(t,\tau)] \ . \tag{4.14}$$

φ is the angle of sun within total viability $Y = W \cdot V$, density-independent viability was constant

$$W(\tau) = W_o < 1 \ . \tag{4.15}$$

Density-dependent viability had the form

$$V(z) = \begin{cases} 1 - p(\frac{1-z}{1-u})^{\beta} \;, & \text{when } z = \frac{A[R]}{A^{\max}} \le u \\ 0 & \text{otherwise} \end{cases} \tag{4.16}$$

$p \le 1$, $u < 1$, β - parameters, that realizes the possibility of describing smooth (small β) and near step-wise (large β) functions of the required types (*Figure 1*). Only background of seeds was considered, as in (4.7) $B(\tau) \equiv 0$.

Finally, we dealt with the system

$$\begin{cases} n(t+1,1) = f \\ n(t+1,\tau+1) = W_o V(z_\tau)\, n(t,\tau) \\ m(t+1,1) = m_o \\ m(t+1,\tau+1) = m(t,\tau) + S_L(m_\tau)\, A(R_\tau) - c m_\tau \end{cases} \qquad \tau = 1,\dots,T-1 \tag{4.17}$$

where V, S_L, A, R, are the functions defined above and for the sake of briefness the following denotations have been used $m_\tau = m(t,\tau)$, $R_\tau = R(t,\tau)$ and $z_\tau = A(R_\tau)/A^{\max}$.

Parameter definition. Species lifespan T was set to = 200 years. The value of α in (4.12) most commonly lies in the interval $0.5 \le \alpha \le 0.8$; we took $\alpha = 0.7$. At the end of the lifespan of coniferous species, the ratio $a_1 = m_L^{\max}/m_{\max} \simeq 0.05$ (Larcher 1975). The mass-surface transition factor for needles was taken as $a^2 = m_L/S_L = 0.15$ [kg raw weight/m^2]. After taking $m_{\max} = 1000$, we can calculate that $a = a_1\, m_{\max}^{1-\alpha}/a_2 = 2.65$; this means $S_L^{\max} = 334$ m^2 and $m_L^{\max} = 50$kg. R_o can be adopted as 1; φ equaled 0.76 [rad]. A typical value of b in (4.13) is in the order of 10^{-1} [kg raw weight/m$^2 \cdot$ yr]; we took $b = 0.15$. The parameter c of unified respiration and decay losses can be found from the demand $m(t) \longrightarrow m_{\max}$ when $t \longrightarrow \infty$ and competition is absent; this gives $a\, m_{\max}^{\alpha}\, b \sin\varphi - c\, m_{\max} = 0$ or $c = 0.034$ [1/kg $\cdot$ yr]. W_o in (4.15) was equal to 0.98053 (by the age $T = 200$, 2% of trees are left). p equaled .5, that is, a moderate jump in V at $z = u$ was allowed.

The values of γ, f, β and u were varied in the search of oscillations. In this way, we experimented with a generalized coniferous tree species having plausible parameter values from measurements and a number of free parameters for the searching of oscillations. Among the latter $\gamma \simeq 0.3-0.8$, f usually varies from some hundreds to thousands, u is near the light compensation level for the whole tree that is $u \approx 0.1-0.3$ and β measures the plasticity of tree response to shortage of resources, a value which is unknown.

The initial conditions comprise zero densities, $n(0,\tau) = 0$ and $m_o = m(0,1) = 10^{-3}$ [kg]; $m(0,\tau) = 0$ for $\tau \ge 2$.

After many numerical experiments we have rested attention on value $\beta = 60$ which relates to all the adduced results. The system was calculated up to $t^{\max} = 2000$ yrs.

The behavior of some important characteristics as functions of γ for parameter values $f = 1000$, $u = 0.15$ is presented in *Figure 7*. Up to $\gamma \approx 0.2$, the system attains stable equilibrium. Near $\gamma = 0.22$ it becomes unstable, and a stable periodic regime arises (*Figure 8*). *Figure 7* shows the dependence on γ of oscillation amplitude $n^{\max}(t,100)$ and $n^{\min}(t,\tau^{\min})$, where $\tau^{\min}$ is the minimum age when the maximum number is at $\tau^{\max} = 100$ (see also *Figure 8* where curves $n(t,\tau)$ are pictured at the time when the maximum goes through age 100). Note (*Figure 7*) the high stability of the oscillation period, $80 \le \theta \le 88$ and value of $n^{\max}$ whereas $n^{\min}$ is greatly reduced.

Behavior of leaf area index $\sigma(t) = \sum_{\tau} S_L(t,\tau)\ n(t,\tau)$. Its time behavior shows the appearance of this dynamical invariant: beyond $t \approx 50-100$, σ assumes a relatively constant value (the relative variations $\Delta\ \sigma/\sigma^{mediate} \approx 0.15$) which is the maximum possible value for the given site and species parameters, $\sigma(t) \approx \sigma^{\max}$. This behavior corresponds well with the situations observed in even- and multi-aged stands. At $\gamma = 0$ (*Figure 7*) – free-growing trees – $\sigma^{\max}$ is very large and equals 115, a totally unreal value for natural populations. However, $\sigma(\gamma)$ then falls quickly attaining reasonable values by the time γ is only 0.1.

All dynamical regimes in three-dimensional parametric space (γ, f, u) are given in *Table 1*, where the period of oscillations, θ, when they exist, is also shown. When the oscillations are quasi-regular, we adduce the observed interval of θ. It can be seen that low values of γ, f, u promote a stable behavior, as their values increase the system becomes unstable and finally falls into a stochastic regime.

Table 1: Oscillation period $\theta(\gamma,f,u)$ and the type of dynamical behavior in (4.17).

	$u = 0.1$			$u = 0.2$		
γ / f	0.2	0.4	0.6	0.2	0.4	0.6
500	SE	SE	SE	SE	86	86
1000	SE	SE	85	86	82	QO,43–71
2000	SE	82	82	83	QO,52–68	QO,49–66

SE = stable equilibrium
QO = quasi-regular oscillations

Among the effects discovered the greatest interest was aroused by the appearance of a parametric invariant (*Figure 7*)

$$J = \gamma \cdot \sigma(\gamma) \simeq \text{const} \ . \tag{4.18}$$

Its appearance is qualitatively comprehensible: $J = \gamma\sigma$ equals the amount of light absorbed per unit area of stand. In addition, it shows the existence of negative feedback between light absorption ability and developed leaf surface that leads to an approximately constant efficiency of light usage. *Table 2* presents the values of σ, J in three-dimensional parametric space taken for $t = 2000$.

The appearance of another invariant $\theta(\gamma,f,n)$, when oscillations are strictly periodical (*Figure 7* and *Table 1*), does not provide for a simple interpretation however.

Table 2 also shows an approximate constancy of σ as a function of seed migration, f, under a given γ, u. Here we are witnessing a 'habitat-saturation' effect which is observed in real ecosystems and explained, as above, by maximum light resource utilization – the overall quantity of foliage cannot exceed a certain limit specified by crown morphology and physiological parameters. The effect was also studied in Korzukhin et al. (1988).

Numerical experiments showed that a large curvature of viability function $V(z)$ (4.16) is essential for the appearance of the oscillations. The influence of p, u, β can be seen from value of derivative at $z = u$: $V'(z)|_{z=u} = -p\beta/(1-u)$.

It is worth mentioning that the used value of $\beta = 60$ yields a 'near-step' function $V(z)$ which is close to purely step-wise survivability functions which are used in many forest models (see review in Section 2.2.). It seems interesting to show the dynamics of formation and passing of the first age wave, which is of great interest for forest ecology

Table 2: Dependence of leaf area index σ (first number) and invariant J (second number) upon system parameters.

	$u = 0.1$			$u = 0.2$		
γ / f	0.2	0.4	0.6	0.2	0.4	0.6
500	7.6 1.52	4.4 1.76	3.1 1.86	7.0 1.40	3.2 1.28	2.4 1.44
1000	8.9 1.78	4.8 1.92	3.4 2.04	6.3 1.26	3.4 1.36	2.6 1.56
2000	9.5 1.90	4.9 1.96	3.6 2.16	6.9 1.38	3.9 1.56	2.5 1.50

regardless of the question of oscillations. The first wave is much higher and narrower than the succeeding ones (*Figure 9*). One can see that at $t = 100$, the system is on the edge of the next wave generation.

5. FROM STAND TO FOREST; ADDITION OF ABOVE-GROUND SPECIES

Up to this stage, we have discussed stand dynamics only, which is a serious contraction of real forest composition. However, although trees can dominate in certain senses, e.g., in terms of the proportion of live ecosystem biomass, essentially they can depend on other species. Among these, the above-ground plant species such as grasses and mosses are most important for boreal forests because they provide the boundary conditions for tree regeneration. In this aspect, trees as a life form exhibit an apparent weakness in their regeneration strategy: many trees suppress mosses and grasses and simultaneously their own seedlings. Sparse stands allow seedlings to grow but also promote their competitors. The interplay between these extremes can lead to interesting dynamical scenarios. Below, we describe some of the model embodiments of a simplified ecosystem consisting of trees and mosses as an example of a two-life form system. Modeling activity in this field is very limited compared with tree systems only, so we can adduce only a few results.

5.1. Modeling of Moss Dynamics

Many dark-coniferous boreal forests are characterized by a noticeable moss organic layer on the forest floor. The thickness of this layer, taking into account both live and dead parts, is up to 30 and 50 cm. The layer is an important structural component of a forest, controlling energy flow, nutrient cycling, water relations, and, through these, stand productivity and dynamics (Bonan and Shugart 1989). For example, soil temperatures and depth of permafrost are directly related to the thickness of the layer. Another example is the dependence of the viability of different types of tree seeds on moss layer thickness (*Figure 10*) which will be discussed below.

First, let us consider only live moss. The simplest description of its growth can be made in terms of carbon balance using variable μ – green moss biomass, [kg/m^2]:

$$\dot{\mu} = S_\mu A_\mu(R_\mu) - c\mu \ , \qquad (5.1)$$

where respiration and decay are assumed to be proportional to μ, R_μ denotes mean light falling per unit leaf area, A_μ is specific assimilation, and leaf area S_μ can be taken as proportional to μ, $S_\mu = a_\mu \mu$. The central idea of this model is that moss growth must be auto-restricted, that is, equation (5.1) must give $\mu \longrightarrow \mu^{\max}$ in the absence of trees and other competitors. If we consider light extinction in a relatively thin moss layer with thickness h and a vertical profile of light $R_\mu(h)$, then, approximately,

$$R_\mu \simeq R(\frac{h}{2}) \simeq R_{\mu o} e^{-\gamma S_m/2} \quad , \tag{5.2}$$

where $R_{\mu o}$ is the light at the top of the layer. If we suppose that A_μ is proportional to R_μ,$A_\mu = bR_\mu$ this gives us a simple equation of moss layer growth

$$\dot{\mu} = a_m \mu b R_{\mu o} e^{-\gamma a_\mu \mu/2} - c\mu = pe^{-q\mu} - \mu \quad . \tag{5.3}$$

For sustainable existence of moss, p must be greater than c. This model coincides with that proposed for grasses by McMurtrie and Wolf (1983). A more realistic model was developed by Bonan and Korzukhin (1989) where the second moss variable ν (dead moss biomass [kg/m^2] and also the usual light curve for assimilation were taken into account:

$$\begin{cases} \dot{\mu} = S_\mu \dfrac{a_1(R_\mu - a_3)}{1 + a_2 R_\mu} - c_1\mu - c_2\mu \\ \\ \dot{\nu} = \qquad\qquad\qquad c_1\mu - c_3\nu \quad . \end{cases} \tag{5.4}$$

In this equation, c_1 is the specific decay rate of live moss, c_2 is its respiration losses, c_3 is the specific oxidation rate of dead moss, a_1, a_2 are light curve parameters, and a_3 is the competition point. The model was identified with the help of actual ecophysiological (Larcher 1975) and field (Van Cleve et al. 1983) moss data.

5.2. Moss-Trees System Modeling

The principal components for the construction of various moss-tree systems have been identified in previous parts of this paper. For example, we may join the age-distributed tree model (4.7) with the simplest moss-growth equation (5.3).

In the simplest case, moss-tree interactions are expressed a) in terms of dependence of initial light flux reaching moss $R_{\mu o}$ on tree leaf area σ: $R_{\mu o} = R_{\mu o}(\sigma)$. These arguments, μ and σ, interconnect tree and moss dynamics.

Whereas the full model (4.7) + (5.3) is difficult to analyze, some qualitative properties can be demonstrated on the basis of its simplified version. Let us take one generalized variable N (total number of trees) and consider only seed background. Then we shall have a very simple tree-moss model

$$\begin{cases} \dot{N} = V(\mu)f - N \\ \\ \dot{\mu} = (pe^{-KN-q\mu} - c)\,\mu \quad , \end{cases} \tag{5.5}$$

where K is proportional to average single-tree leaf area multiplied by extinction coefficient for trees. In this approximate description N can be changed to total tree biomass M. The behavior of this system is typical of two-dimensional systems with "competitive" interactions, which are encountered repeatedly in ecological modeling (e.g., McMurtrie and Wolf 1983).

First consider the case only of suppression form of function $U(\mu)$ – ***Figure 10***. Let us take $U(\mu) = 1 - \mu/\mu*$ when $\mu < \mu*$; otherwise $U(\mu) = 0$. Simple qualitative analysis of system (5.5) gives us four standard situations. By denoting $r = \log\,(p/c)$, we have:

1. If $kf > r$ and $q\mu * > r$, we have one stable equilibrium (f,o), that is, trees outcompete moss.

2. If $kf < r$ and $q\mu * > r$, we have one stable equilibrium (N^o,μ^o), where $N^o < f$, $\mu^o < \mu *$, that is moss and trees coexist; N^o, μ^o can be found from the system

$$\begin{cases} kN + q\mu = r \\ N - f(1-\mu/\mu *) = 0 \ . \end{cases}$$

3. If $kf > r$ and $q\mu * < r$, we have two stable equilibria (f,o) and $(o,r/q)$ which are realized depending on initial conditions $N(o),\mu(o)$.

4. If kf, r and $q\mu * < r$, we have one stable equilibrium $(o,r/q)$ that is moss trees.

The case of a nonmonotonous function $U(\mu)$ (***Figure 10***) adds the possibility of two stable states coexistence – (N_1^o, μ^o) and $(N_2^o,0)$.

Now let us imagine a movement along an environmental gradient from dry conditions which are favorable for tree growth and unfavorable for moss (f is large, p is small), to wet conditions where the reverse is true. In this case, system (5.5) will describe the consequences of moving from states 1⟶2⟶4 or 1⟶3⟶4, that is, the transition from temperate forests without moss to tundra without trees, passing between these extremes through the possibility of tree-moss coexistence (boreal forest) – ***Figure 11***.

There is absolutely no doubt that any generalization of this qualitative system (e.g., equations (4.7) + (5.4)) will retain this transition effect.

In a more realistic simulation, but not mathematical, model (Bonan and Korzukhin 1989) this type of tree-moss behavior was actually discovered along a cold–wet to hot–dry environmental gradient. The sites were typical of central Alaska and were dominated by black and white spruce, white birch and trembling aspen, plus sphagnum mosses. The two-compartment moss model (5.4) was used. Functions of seed germination suppression, $U_i(M)$ for each tree species i were reconstructed from field data; here $M = \mu + \nu$ is the total moss biomass. The dynamics of the trees were described using a usual gap-modeling technique. Field observations along the gradient supported model results, see the cited work for details.

6. CONCLUDING REMARKS

In this paper, two general aspects of modeling are considered. First, the results of developing and running models of forest dynamics at the population level, based on the results of certain dynamical equations, are given. In principle, this approach is equivalent to the gap-model approach described in Shugart (1984). There does not appear to be any property of forest dynamics at the population stand, or ecosystem level, that cannot be adequately described and explored by means of models at the population level. It would appear that until the problems of determining spatial heterogeneity at the individual-tree scale have been overcome, the question of which approach should be used is simply one of technical suitability (parameter estimation, calculation time, etc.) and not of principle.

The second aspect relates to modeling methodology. We attempted to illustrate how, in our opinion, the approach to modeling should develop. At present, modeling appears to be more akin to art than science with each model being more or less specific, and each modeler choosing his own empirical rules of advancement. The view we advocate can be expressed as "Try to use simplicity before sinking into complexities." For example, if the requirement is to analyze the behavior of overall population-level characters these should, if possible, only be used as state variables, without size or age distributions, individuals, etc. The model should be made more complex only if it does not give the required information. If single-level, horizontal crowns give reasonable results, these should not be changed to vertically distributed ones. If a single-variable equation of trajectory of tree growth is required as output, use a single-variable equation of growth until it gives you what you want. Many examples of unnecessarily complicated approaches are found in forest and ecology modeling literature.

In general, much modeling is performed on a 'trial and error' basis. Usually, the ecological mechanisms and the level of detail needed to be included in order to achieve the required information on a population or forest system, are not known. As yet, no attempts have been made to answer this basic question, although the whole issue is central to any modeling. Only when the necessary-sufficient relationships are known can one affirm that property A is explained by property B, that is, B is the reason for A's origin. Only a model constructed on this basis gives an 'explanation' and can produce accurate and reliable results; all others are incomplete to some degree. In this connection, we would like to emphasize the importance of parameter adjustment using the model itself (e.g., by means of the mean squares technique). Only this procedure, as opposed to simple parameter input in an imitational manner, can result in the full appreciation of a model's possibilities and quality. This is not a whim of mathematicians; not only is it a way of improving a prognosis but also of finding the range of a model's applicability.

Forest modeling is currently in an active phase of its development. Both the expectations and the resources involved are high, and we believe that a certain degree of methodological accuracy should be sought in order to optimize output and to make the results more reliable.

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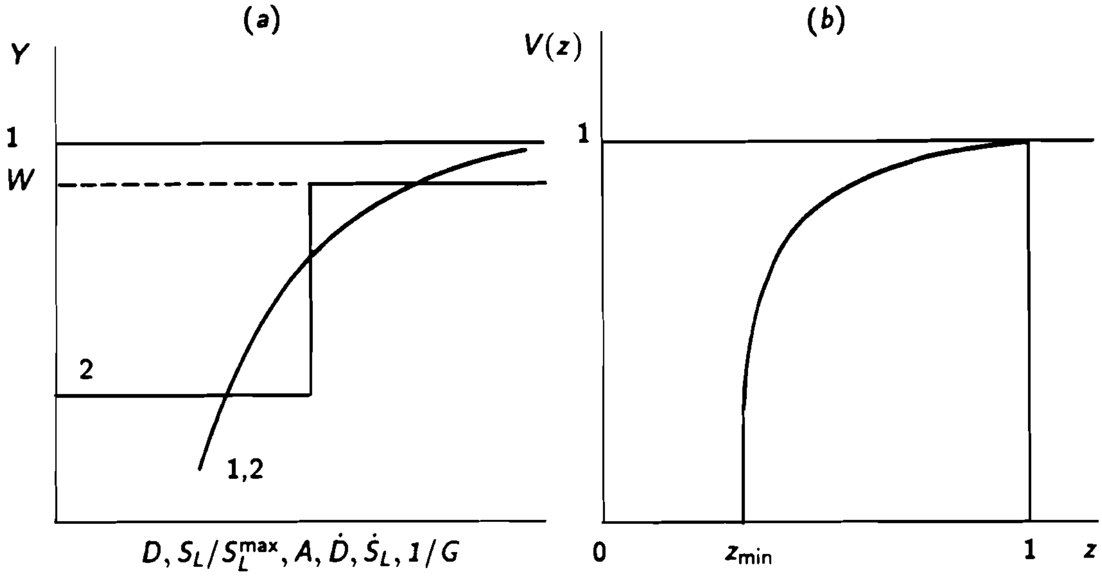


Figure 1: Qualitative behavior and arguments of viability function Y for a single tree. (a) empirical (1) and model (1, 2) forms following field data and model (see text for references and denotations). W – viability of mature, maximum defenced tree. (b) quality behavior of density-dependent viability components, V, on argument $z = A/A_{\max}$; V is recommended for 'base model 1' (Section 3.3) and used in 'base model 2' (Section 4.3); $z_{\min} = A_{\min}/A_{\max}$ where $A_{\min}$ is maintenance respiration of leaves or whole tree.

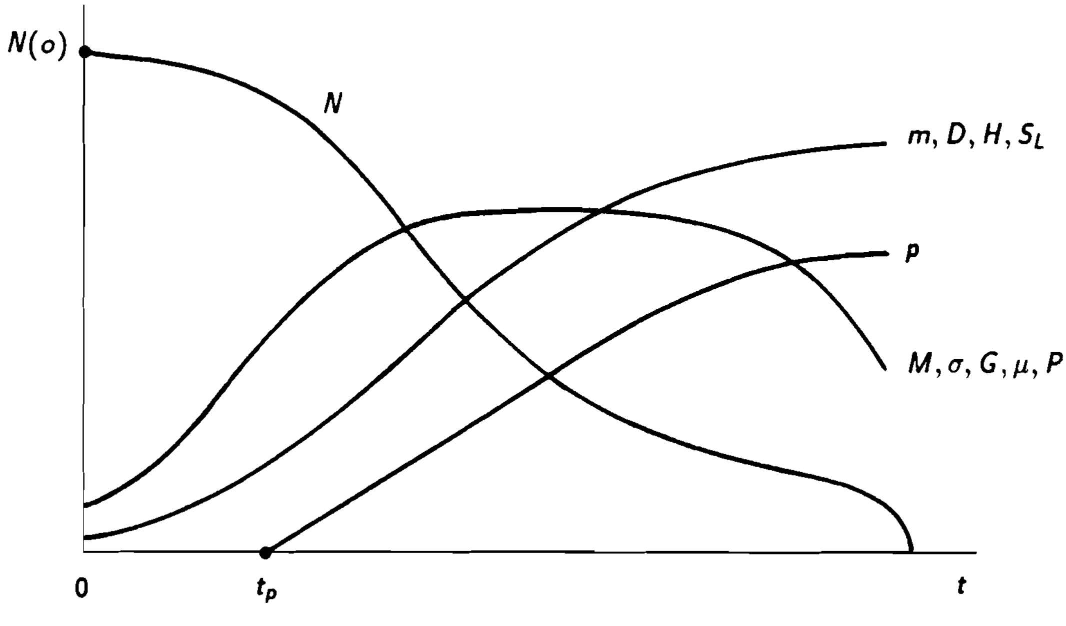


Figure 2: Qualitative dynamics of major variables of even-aged systems; curves with the same type of behavior are unified: $\mu = mN^{3/2}$ (see text for denotations).

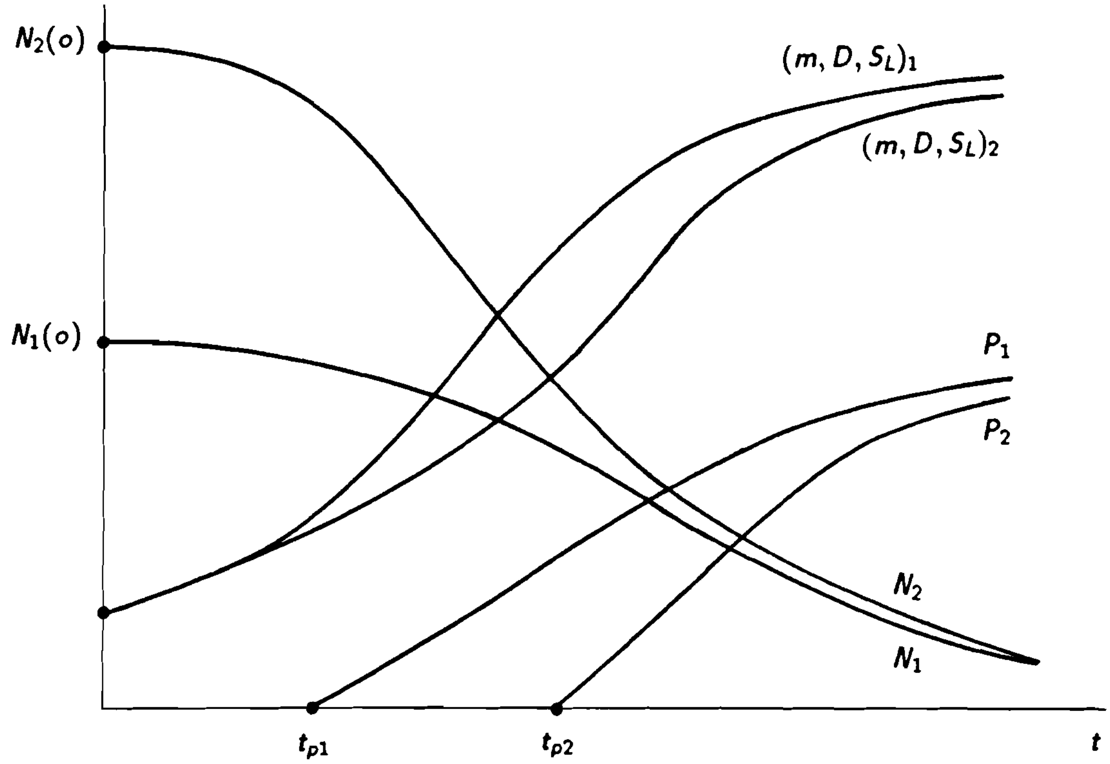


Figure 3: A set of even-aged system trajectories obtained under various initial densities (see text for denotations).

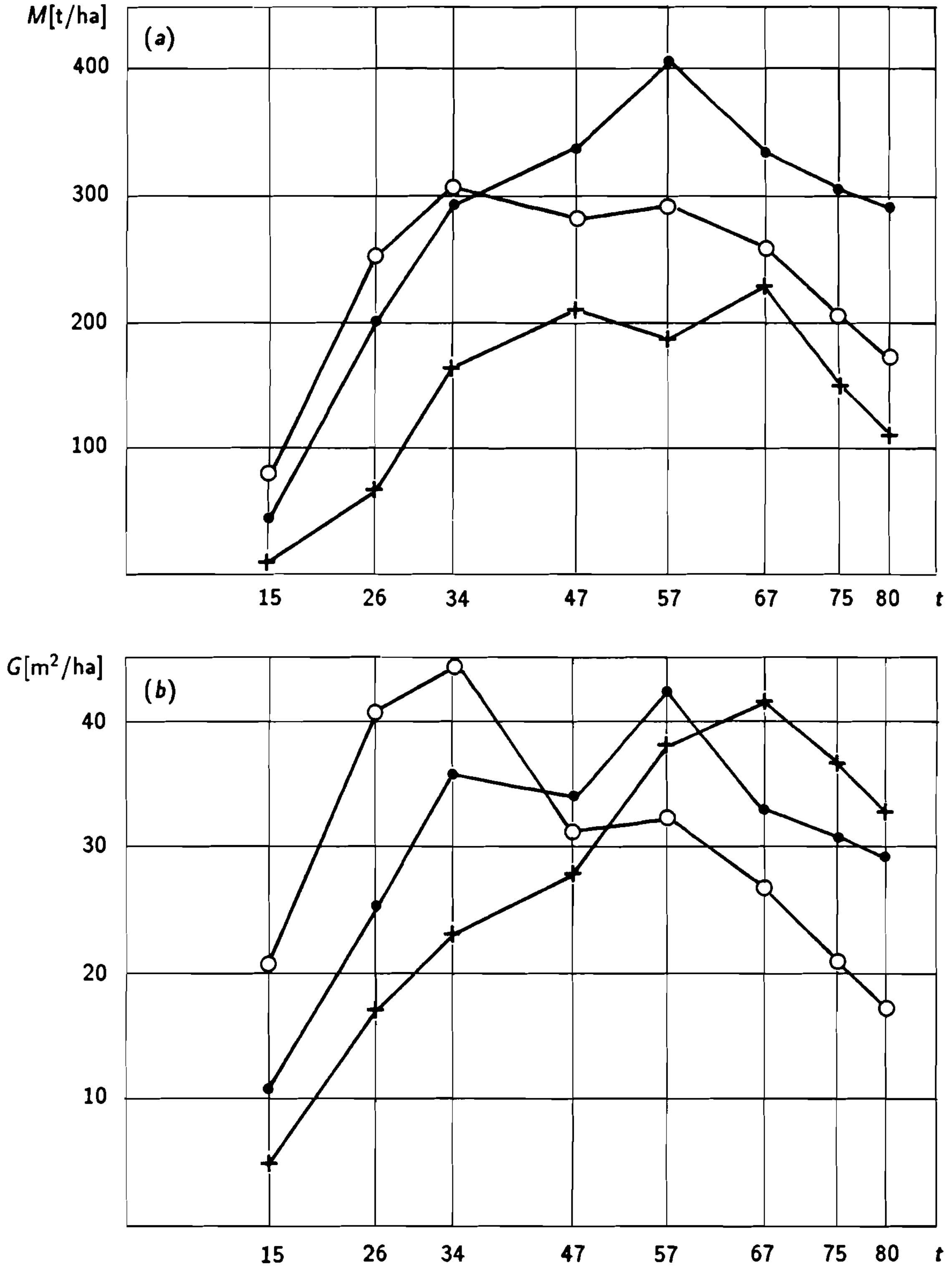


Figure 4: Trajectories of population biomass M – (a), and cross section area G – (b) (which is proportional to σ under initial densities $N_1(o) = 1000$ – (+), $N_2(o) = 2400$ – (•), and $N_3(o) = 10000$ – o); data from permanent plots with *Pinus sibirica* in Moscow region. "Overcrowding" effect consists of $M_3^{\max} < M_2^{\max}$ under $N_3(o) > N_2(o)$, whereas all $G_i^{\max}$ are approximately equal, only $t_{G_i}^{\max}$ changes.

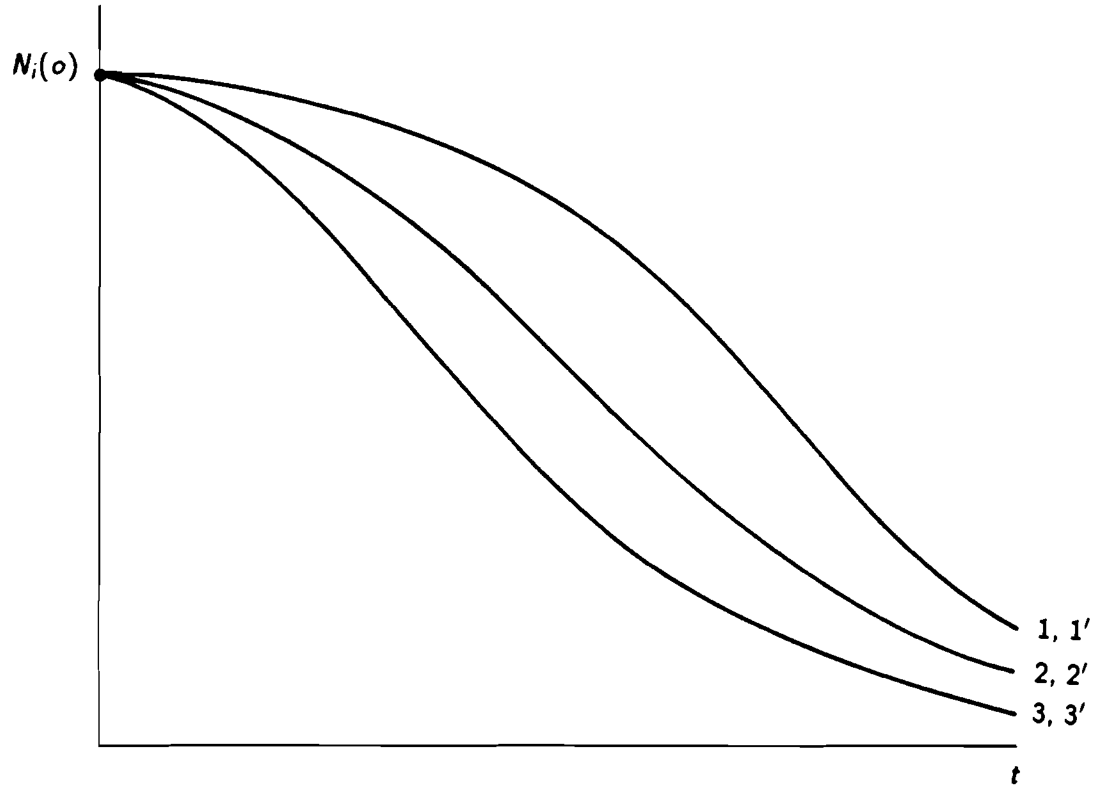


Figure 5: Given the equal initial numbers of trees, $N_i(o)$, $N(t)$ falls rapidly for ameliorated site conditions $(1 \longrightarrow 2 \longrightarrow 3)$ and with decreasing shade tolerance $(1' \longrightarrow 2' \longrightarrow 3')$.

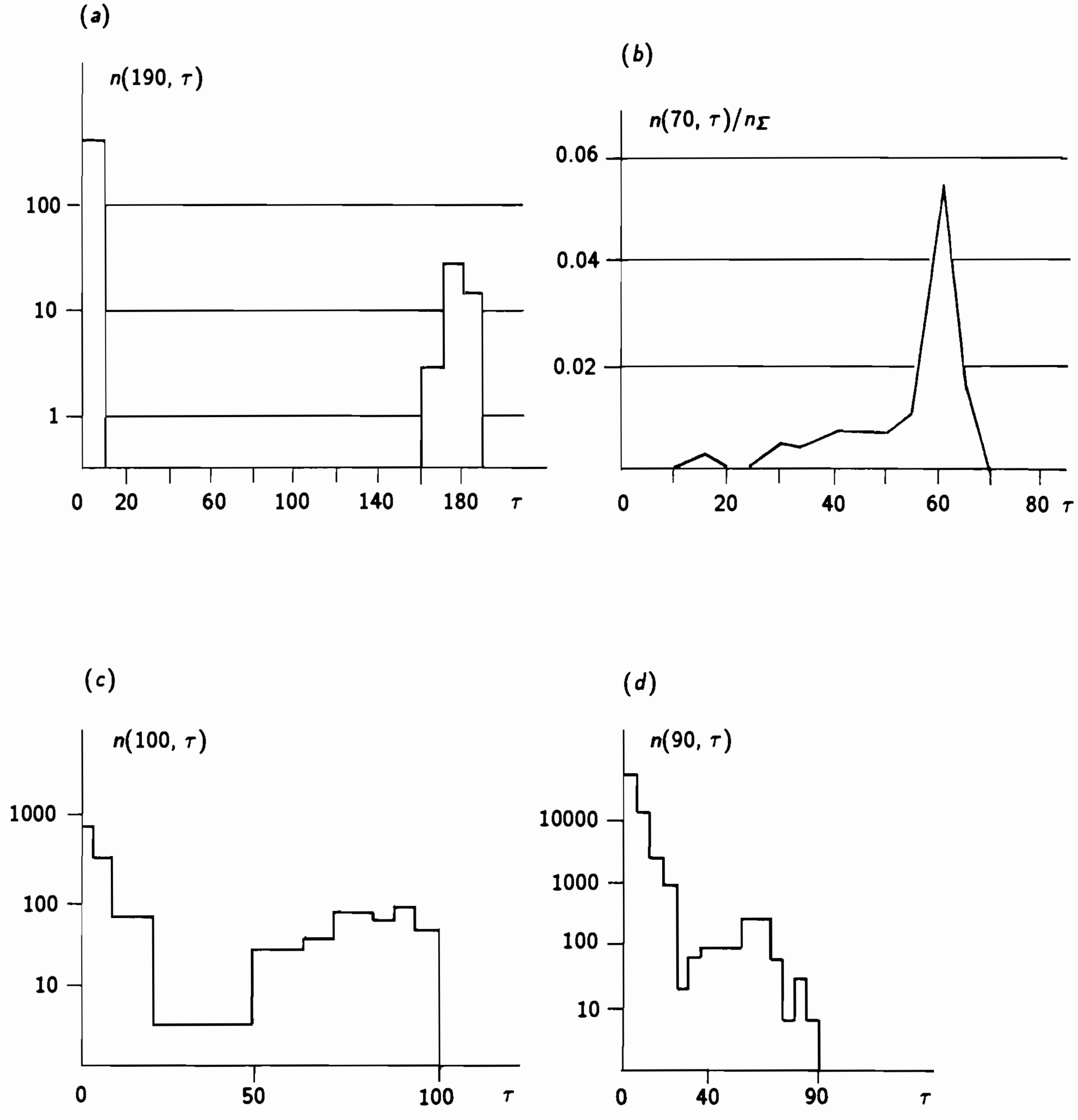


Figure 6: "Age waves" emerging after major forest cover disturbance in sufficiently dense stands. $n(t,\tau)$ is the number of trees in age interval $\Delta\tau = 1$ under age τ, t is moment of observation (equal to time since disturbance). Cases of strong suppression of juveniles by mature canopy: (a) – post fire succession, ***Pinus sibirica***, West Siberia (Semetchkin 1970); (b) – post cutting succession, sum of oak, maple, and birch, New England (Oliver 1978). Cases of weak suppression: (c) – post fire succession, sum of spruce, ***Pinus sibirica***, and fir, West Siberia (Korzukhin et al. 1988); (d) – post fire succession, mixed oak forest. Appalachian Mountains (Ross et al. 1982).

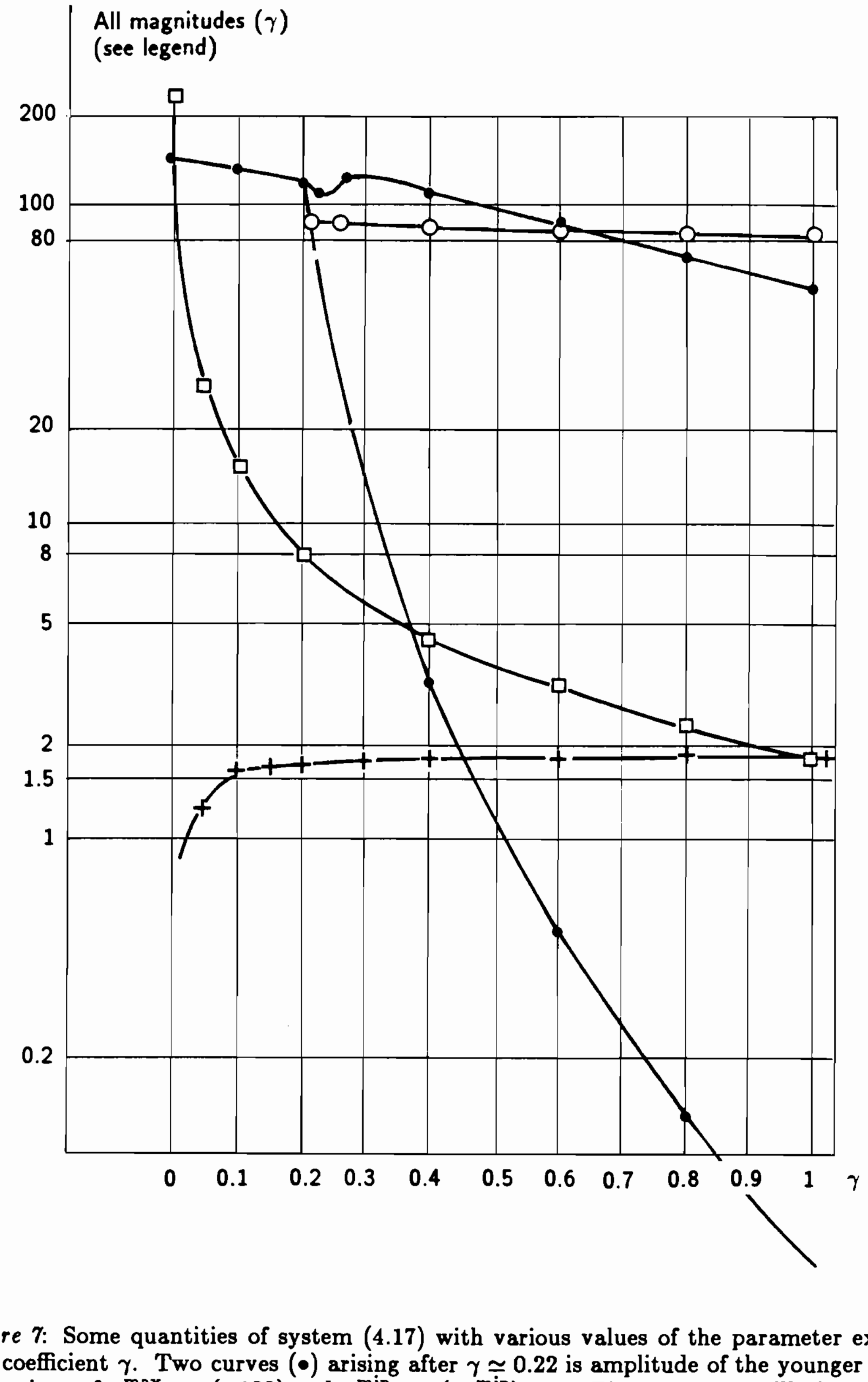


Figure 7: Some quantities of system (4.17) with various values of the parameter extinction coefficient γ. Two curves (•) arising after $\gamma \simeq 0.22$ is amplitude of the younger wave – meanings of $n^{\max} = n(t,100)$ and $n^{\min} = n(t,r^{\min})$ – see *Figure 8*. *o* – oscillation period $\theta(\gamma)$, □ – leaf area index $\sigma(\gamma)$ in $T = 2000$, + – value of $J = \gamma \cdot \sigma(\gamma)$.

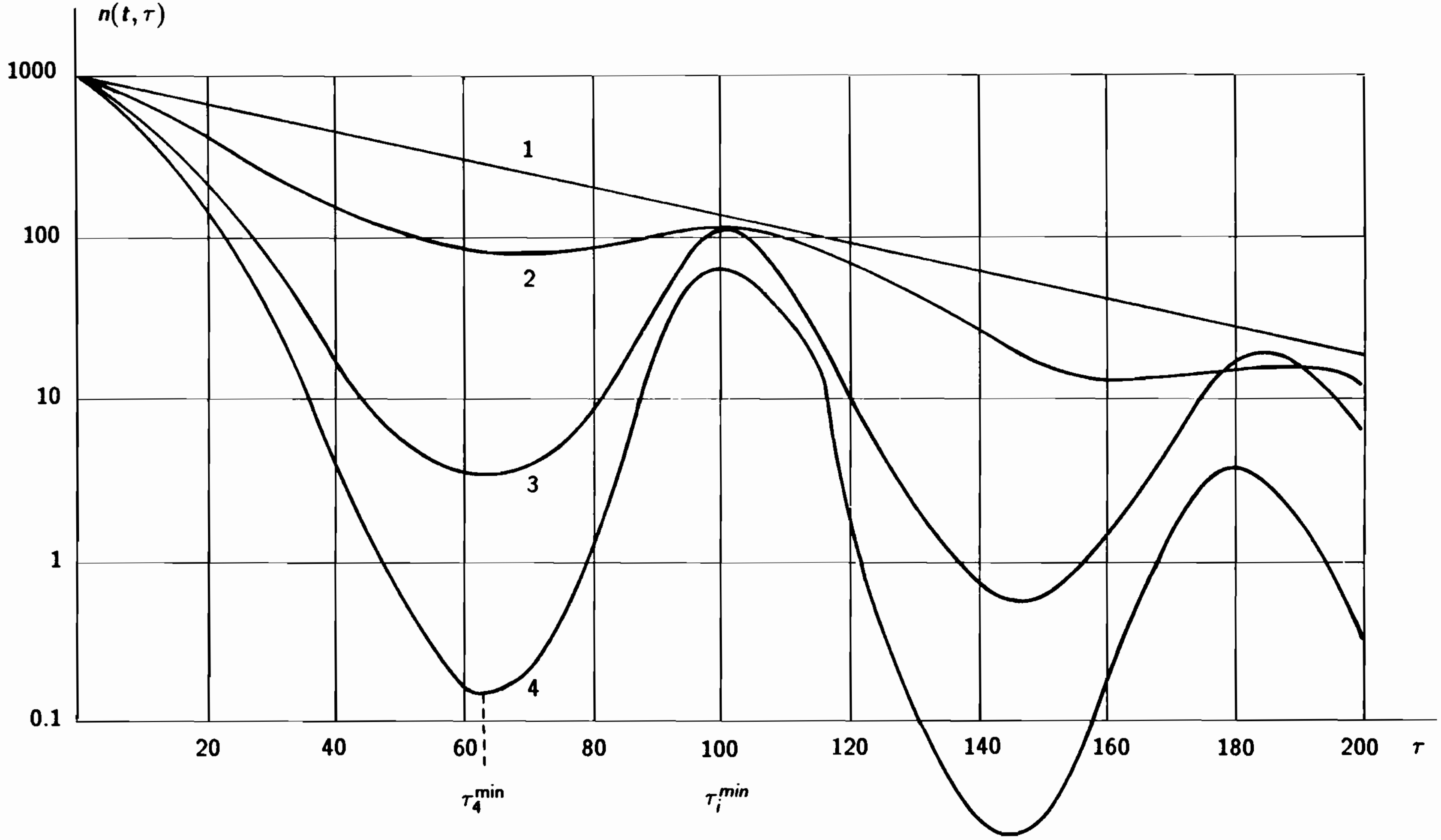


Figure 8: Age distributions of tree numbers $n(t,\tau)$ - solution of system (4.17) under various γ; 1 - stable distribution for $\gamma = 0$, $n(\tau) = 1000 \cdot \exp(-0.0197\tau)$; 2, 3, 4 - stable oscillations for $\gamma = 0.226, 0.4, 0.8$; curves are taken in time moment t when maximums were going through age $\tau = 100$ (see text for parameter values).

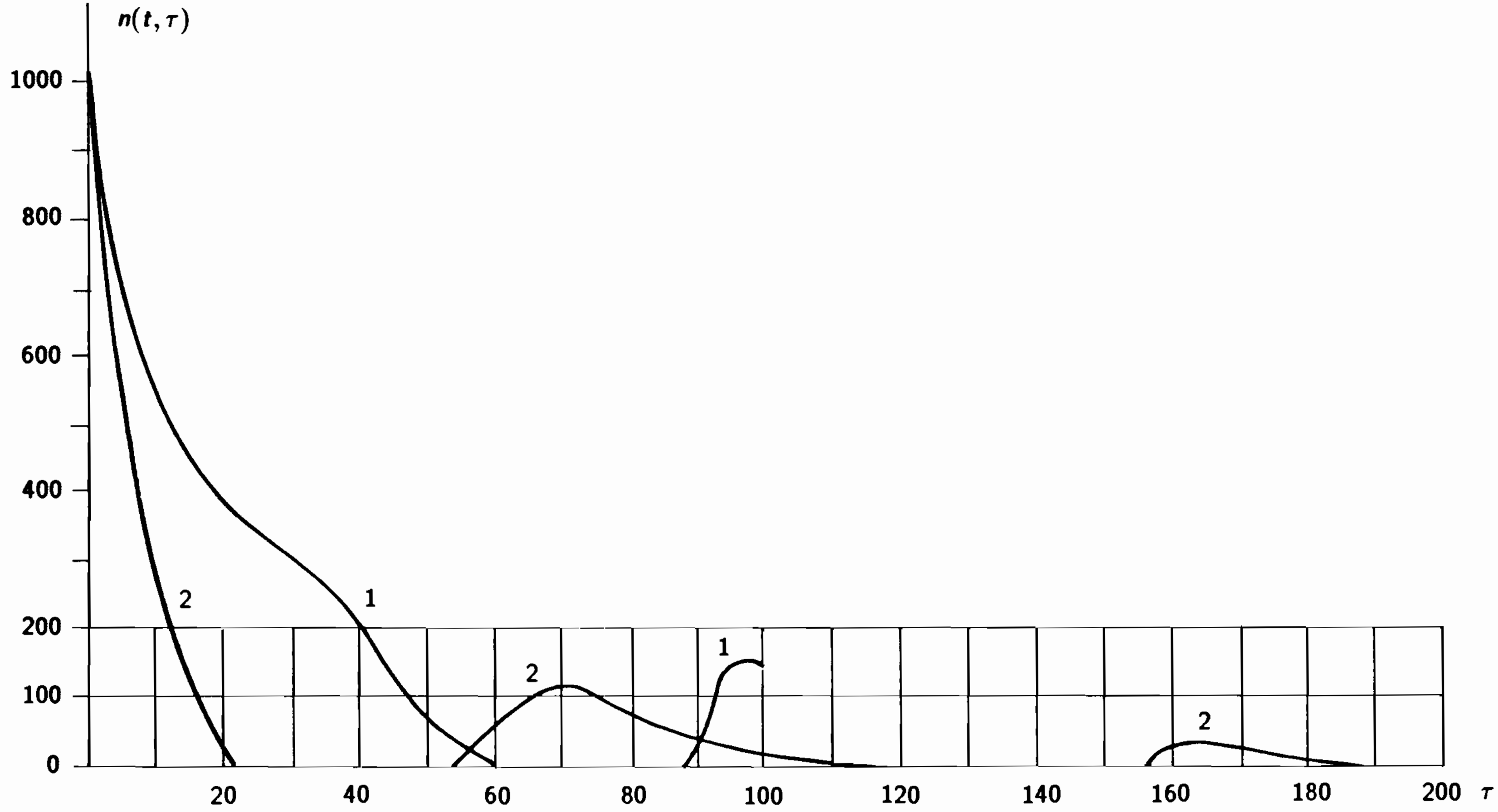


Figure 9: Solution of system (4.17) under $\gamma = 0.4$ and $u = 0.2$; 1 – first “age package”, 2 – stable oscillations.

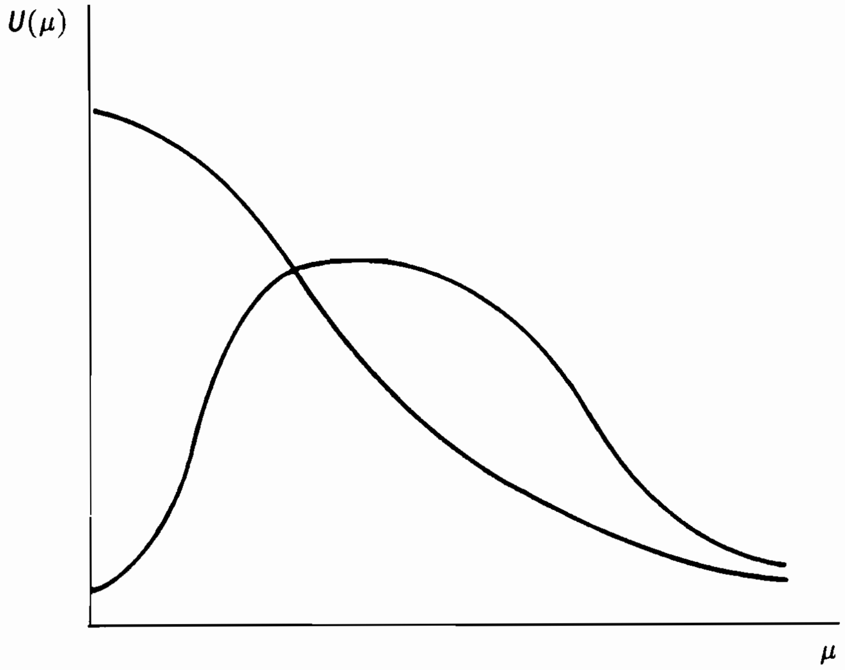
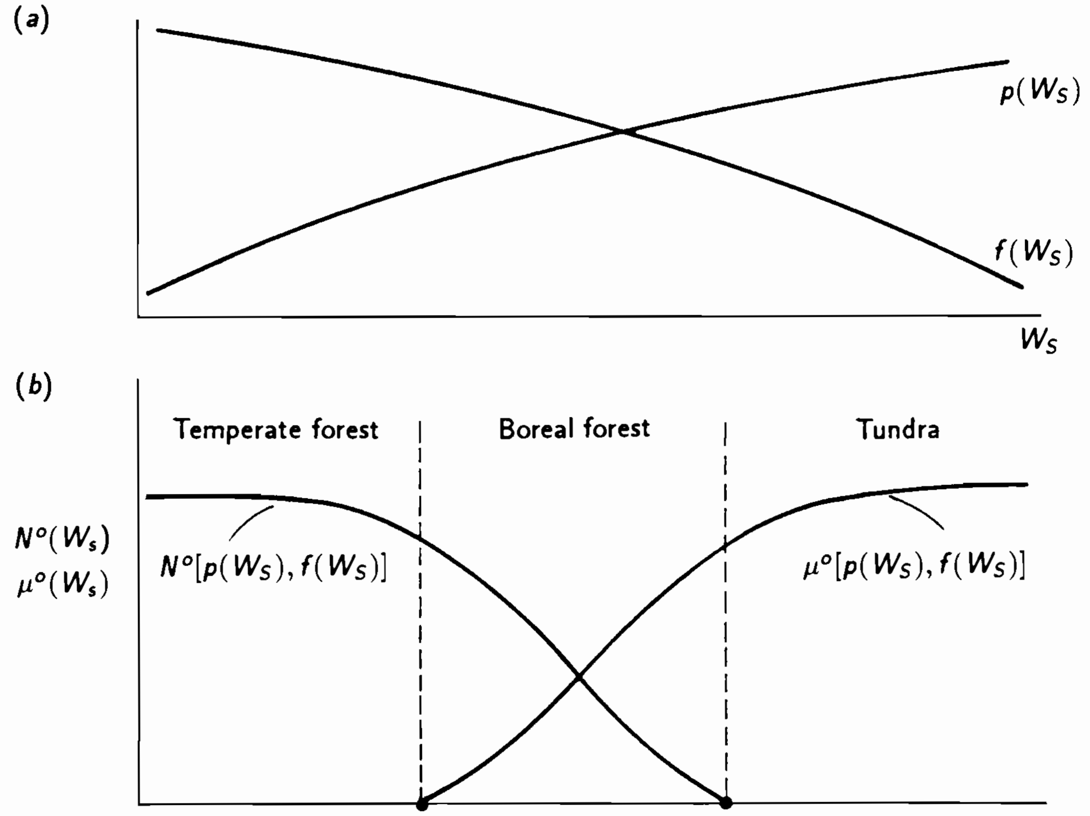


Figure 10: Qualitative dependence of seed survival and germination. U, on moss biomass; μ (or thickness) for boreal tree species. a – small seeds (birch, spruce), b – large seeds, in particular *Pinus sibirica*, whose seed viability is maximal under a certain moss thickness (summarized in Katayeva and Korzukhin 1987).



State 1: $\ln \frac{p(W_S)}{c} < kf(W_S) < q\mu*$

State 2: $kf(W_S) < \ln \frac{p(W_S)}{c} < q\mu*$

State 4: $kf(W_S) < q\mu* < \ln \frac{p(W_S)}{c}$

Figure 11: Parametric evolution in tree-moss system (5.5): if one considers p, f as monotone functions of soil moisture W_S – (a), then steady states of (5.5) – $N^o(W_S)$, $\mu^o(W_S)$ realize trajectories – (b), which can be interpreted as different types of tree-moss ecosystems disposed along environmental gradient (case of monotonous $U(\mu)$, consequence of states 1⟶2⟶4). Underneath *Figure 11b* we adduce the conditions of each state of realization in system (5.5).