Working Paper

ECOPHYSIOLOGICAL MODELS OF
FOREST STAND DYNAMICS

M.Ya. Antonovsky
F.S. Berezovskaya
G.P. Karev
A.Z. Shvidenko
H.H. Shugart

WP-91-36
September 1991

ECOPHYSIOLOGICAL MODELS OF
FOREST STAND DYNAMICS

M. Ya. Antonovsky
F.S. Berezovskaya
G.P. Karev
A.Z. Shvidenko
H.H. Shugart

ABSTRACT

It is well known that woodlands play a crucial role in stabilizing the natural environment. They greatly influence and regulate hydraulic cycles, and thus the flow of waters and local humidity conditions. They also filter air pollutants, thus protecting vulnerable soils and water bodies within forested watersheds. Therefore, as global belts of Boreal, Moderate and Tropical Forests actively take part in different biogeochemical and physical cycles in the biosphere, and play an extremely important role in the exchange of heat and moisture between the atmosphere and continents, an assessment of the forests in different time and spatial scales is of considerable value to the life of the human society.

The systems approach permits us to look at these interrelationships in a comprehensive way and to see many negative and positive feedbacks which, together, provide a dynamical equilibrium of the waves in the all forest belts mentioned above (including others organic and inorganic waves, such as waves of insects, diseases, fires etc.).

In the course of its existence IIASA has constantly been occupied with different aspects of the forest life. From time to time international working groups are formed on a IIASA base to examine the different aspects of the forest and forestry dynamics.

The most recent example is a book on systems analysis of the Boreal Forest Dynamics, published by Cambridge University Press (Shugart et al., eds., September 1991). A group of American, European, Canadian and Soviet authors have worked together through a collaborative network. The products of the group include a general boreal forest model (which is currently being used to evaluate the potential effects of global climate change on the North American Boreal Zone); models on fire dynamics, seed dispersal, permafrost dynamics, herbivory and CO_2 flux have been developed, providing a general modeling framework for simulating patterns and processes in the boreal zone.

The present paper may be considered as some additional input to the problem, in the form of Ecophysiological Models, which were partially missing in the above-mentioned book. The paper partially intersects with the contents of the book, but from a different angle, especially as many papers considering the Russian view of the problem are added.

The book on "System Analysis of the Boreal Forest Dynamics" and this outline stress the necessity of the development of a collaborative research effort to continue the development of computer models of the boreal forest (analogue to the GCM -- see, for example, Shugart, Bonan), and the so-called analytical models (analogue to the Global Average Models (GAM) -- see for example Antonovsky, Korzukhin) in response to environmental change.

Assessments of anthropogenic stress on forests that show such complex dynamics are daunting. There is a clear need for a continuation of process-oriented comparative studies in polluted and non-polluted regions of the boreal forests to better understand these effects. It is clear from the reviews of actual observations and experimental evidence from the boreal forest and from the boreal forest models that the landscape response of boreal forests to stress is complex and not easily obtained from

static measurements. Furthermore, the feedback complexities in the boreal forest ecosystem suggest that a multiple research program of experimentation, modeling and observation may lead to a better understanding of the forest dynamics under stress or novel situations than one-dimensional research programs.

ECOPHYSIOLOGICAL MODELS OF
FOREST STAND DYNAMICS

M.Ya. Antonovsky   IIASA, Austria

F.S. Berezovskaya   VNIIClesresource, Moscow

G.P. Karev   Council of Cybernetics,
                         Academy of Sciences of the USSR,
                         Moscow

A.Z. Shvidenko   VNIIClesresource, Moscow

H.H. Shugart   University of Virginia, USA

INTRODUCTION

The present survey is dedicated to description of a number of approaches allowing to model dynamics of tree, forest stand, tree or forest association on the basis of ecophysiological models, both analytical and simulative. As distinctive peculiarity of such models, one may regard application of dependences and variables that are interpreted directly on the ecophysiological basis. It allows to verify and to identify models according to the data from observations, as well as to test ecophysiological hypotheses assumed as a basis of one or another model (unlike phenomenological models). The detailed simulation models are characterized by taking into account large amount of variables

and parameters of the modeled object, as well as by selection
of coefficients for precise (as far as possible) description
of the concrete object (tree of certain species, forest within
given geographical and climatic zone) with the following fore-
casting for comparatively short times. Size of model doesn't
usually allow to analyse influence of many parameters upon
qualitative behaviour of system. For this purpose one applies
analytical models describing dynamics of the essential variables
and parameters. These models don't aim at rendering precise
dynamics of the concrete object, but they allow to find out
qualitative peculiarities of behaviour, its possible changes
depending on variations of parameters, as well as to study
utmost conditions and changing of spatial boundaries. It seems
promising to apply jointly both analytical and simulation eco-
physiological models when analytical models are regarded as
certain subblocks being parts of simulation models that makes
it possible to replace the real experiment by the numerical one,
to adapt model to the modeled object, as well as to forecast
feasible situations.

We dwell at length on the description of structure and
features of ecophysiological models belonging to analytical
type which are given main consideration in the present survey.
It is usually a dynamical equation worked out on the basis of
balance relations. As one of the values (that have physiological
interpretation for tree objects), one consideres often photo-
synthetic rate. The relationship with ecological conditions is
realized by means of indicating dependences of physiological
values on accessible resources of the productive process (in
case of photosynthesis, for example, it is dependence on amount
of accessible light, on accessible moisture or mineral sub-
stances, etc.), as well as on concentrations of pollutants or
other factors which influence the productive process. Transi-
tion from the level of individual plant to the phytocenosis
level is realized with the aid of dependence (which is obtained
in a theoretical or a simulation way) for amount of resource
which falls to the share of one plant as a result of competition
with other plants. The processes of competition are described by

a physiologically interpretable mathematical model. Transition
to the level of tree association is characterized by indicating
of relationships between individual components of this associa-
tion (perhaps, between individual loci, cenoses, etc.). We may
note that regional models (developed for accomplishment of the
territorial forecasting) may (as a matter of fact) not be eco-
physiological ones in the narrow sense of this word, though
these models operate with such ecological conceptions as locus,
succession, etc.

By such approach, statistical models, as well as numerous
regressional and empirical models which may be very helpful for
practical tasks prove to be of little use because they are not,
in the main, "explaining" ones. We may note, however, that such
dependences are often included into ecophysiological models in
the capacity of submodels or some limiting values. One of the
reasons for such methods may consist in the following.

Specific character of systems at each level of modeling is
determined not only by differences of the studied objects and
by depth of modeling (Poletayev) but also by differences of
characteristic times and scales. Hierarchy of times is expres-
sed mathematically with the aid of "small" parameter ε : three
characteristic times are singled out, namely slow time $t \sim \frac{1}{\varepsilon}$,
real time $t \sim 1$ and rapid time $t \sim \varepsilon$. Examination of processes
for times of the order 1 corresponds to limiting transition by
$\varepsilon \rightarrow 0$. Then the variables of slow processes are considered as
parameters (on a level with environmental parameters), whereas
the variables of rapid processes are considered as members of
algebraic relation (sustained process) that, perhaps, is simi-
lar to dependence given by the mentioned empirial correlations.

It should be noted that by analytical modeling it is
essential to single out main ("limiting") factors that allow
to go over to the investigating of critical conditions and to
determine boundaries for existence area of the object.

Modeling is playing an ever-increasing role in the development of ecological theory at several scales, from understanding the mechanisms of carbon fixation (Farquhar and Sharkey 1982; Farquhar and von Craemmer 1982) and plant water balance (Cowan 1982, 1986); to scaling of physiological processes to whole plant function (Reynolds et al. 1986); to exploring how ecosystem processes of carbon and nitrogen cycling operate at continental to global scales (Emanuel et al. 1984, 1985). Of particular importance is the role of modeling in exploring phenomenon which occur at spatial and temporal scales at which extensive direct observation and experimentation are prohibitive, if not impossible. Recent examples include the role of spatial and temporal variation in competition on ecosystem functioning (Wu et al. 1985; Sharpe et al. 1985, 1986; Walker and Sharpe 1989), extrapolation of the processes of carbon fixation and water balance to the landscape scale to enable linking ecosystem models with remotely sensed data (Running and Coughlan 1988), and exploring the implications of the evolution of plant adaptations to varying environmental conditions on current patterns of ecosystem structure across environmental gradients (Tilman 1988).

The diversity of extant modeling approaches proscribes the designation of the model of virtually any ecological system. Appropriateness of model structures depend strongly on the objectives of the model users. The scientific challenge in modeling tends to lie on the proper selection of the phenomena that attend a question's solution and that are appropriate to the time and space domain of the problem.

This is an era of increased interest in the function and interaction of the major geophysical, geochemical and ecological systems of the earth. The interest in these large spatial scale studies has had diverse origins: the success of the "International Geophysical Year" of global observations (1957-1958) and a shared comprehension of just how much time has passed since this effort; the characterization of the surface of the earth from an ever increasing availability of images from space; the realization that humans are altering the composition of the atmosphere; a relative warming in international political tensions and the increased likelihood of sustained international scientific exchanges; an improved understanding of the past dynamics of the earth's surface resulting from radioisotope dating and analysis of paleoecological data; and the ramifications of computers with the power to solve complex equations of the fluid motion of the atmosphere and oceans.

The conjunction of these and many other developments have turned the interests of many scientists in different disciplines to the issue of increasing the level of understanding of the earth as an interacting, dynamical system.

The present survey has the following structure. Section 1 contains description of models used when studying development of a tree, as well as information about individual processes associated with this development. Models of even-aged forest stand in conjunction with methods applied by competition modeling are described in Section 2. As model variables, one can regard both numbers of forest stand (or density of numbers) and structural characteristics of the object (mass, area of crown surface, etc.). Examples of described models being applied are also given. In Section 3 processes associated with age structure of stands are described with the aid of so-called "structural

models". Taking into account existence of "multistoreyed and multispecies" objects within these models, as well as existence of specific competition arising within objects of different age allows to go over to constructing of succession models (and then models of tree association on the whole). One of such approaches consists in considering of tree association as the superpopulation of local associations (cenons). Section 4 contains a number of examples of the simulation ecophysiological models. Among them, "window" models and gap-models play the leading part. Section 5 contains descriptions of some approaches to modeling of the spatial dynamics.

1. Growth of separate tree

1.1. Growth of separate free-to-grow tree is described approximately by the so-called "S-like curve" presented at the Fig.1a. In its turn, growth rate is described by the curve shown at the Fig.1b.

Fig.1a

Fig.1b
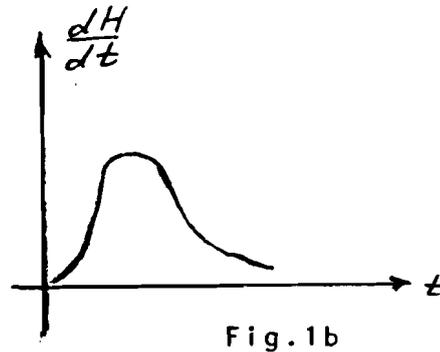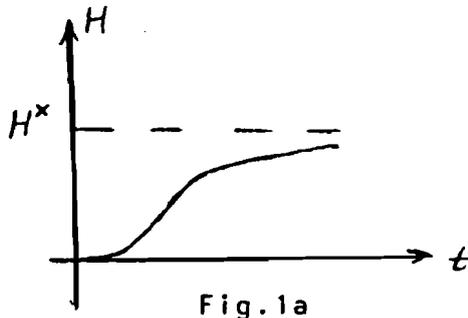
There is a voluminous literature on considering and analysing of such curves which approximate dynamics of different parameters intrinsic to a separate tree (see, for example, monographs by Kuzmichev, 1977, Terskov, Terskova, 1980, etc.). For analytical description of these curves a number of well-known formulae is used, namely:

Tarazaki's function

$$y = a \exp(-b/x) \qquad (1.1)$$

Koller's function

$$y = ax \exp(-Cx) \qquad (1.2)$$

Korsun-Backman's function

$$y = a \exp(b \ln x - C \ln^2 x) \qquad (1.3)$$

Curve presented at the Fig.1a can be also approximated by the function of fractional-rational type

$$y = \frac{ax^n}{1+bx^n} \qquad (1.4)$$

Coefficients which appear in the formulae (1.1)-(1.4) can be chosen so that curves defined by those functions will correspond rather well to the experimental data doing without any penetration into the laws of growth.

An attempt to explain stable relationship between sizes of different organs in the course of ontogeny resulted in the law of allometry being formulated. In accordance with this law, similarity, considered as relationship between individual organs, is kept during their growth and can be expressed by means of power dependence

$$y = ax^b \qquad (1.5)$$

or in the form of basic similarity equation

$$\frac{dy}{ydt} = \frac{adx}{xdt} \qquad (1.5')$$

It is Huxley (1932) whom the fundamental study in this field belongs to.

When modelling relationships between sizes of organs, many authors use allometric dependences. In particular, Kofman (Кофман, 1981) made an interesting attempt to ground the law of allometry in a theoretical way.

In our opinion, utilization of allometric approximations which may be justified by describing of smooth processes is absolutely insufficient for modelling in a critical situation that can be characterized by both change of exponent in formula (1.5) and arising of new dependences. This point of view is confirmed by Schmalhausen's study (1984) who supposed that during ontogeny it would take place the successive change of periods and for every of them growth would be described by own specific equation of the type (1.5). The monograph by Terskovs' (1980) and many other works were devoted to utilization of the step parabolic equation for modelling of growth for forest stands.

Thus, by constructing of power dependences it's important to indicate both characteristic periods when these dependences are valid and the type of external influences.

Let's give some examples of models belonging to the type
$(1.5 - 1.5^1)$.

Diameter increment of tree is given by

$$D = \frac{GD(1-DH/DmHm)}{274+3aD-4bD} \qquad (1.6)$$

where D is the diameter at breast height, H is the height of
tree, Dm and Hm are corresponding maximum values (like a and b,
they are parameters intrinsic to the given species), G is the
maximum rate of growth; it's assumed that $H \sim \sqrt{D}$. This function
is used within the framework of "large" simulation models
JABOWA (Botkin et al., 1972), FORET (Shugart, West, 1977),
KIAMBRAM (Shugart et al., 1980). Rachko (1979) used it as a
submodel to describe behaviour of the forest stand as a whole.
For longer periods of time, physiological processes for function
(1.6) were not taken into account in detail because this func-
tion may be interpreted only in a general way. Oja used this
function quite satisfactorily for his task with a view to
describe growth of spruce fir (Oja, 1984).

1.2. One of the first dynamical and, as a matter of fact,
phenomenological models for free-to-grow trees turned out the
Robertson equation (Robertson, 1923)

$$\dot{M} = K(A-M)M \qquad (1.7)$$

where M is the biomass and A is the respective maximum value,
K=const.

This equation arose from describing of kinetics for the autocatalysis reaction. Perhaps, the use of analogy between the growth of plant and the course of only one reaction might be justified for the reason that despite of variety of chemical and physical processes, both character and rate of growth of plant are determined by one dominant reaction (Hilmi, 1976, Kull, 1986). It should be noted that equation (1.7), under the name of "Verhülst-Pirl equation", is widely applied to describe population numbers within the framework of population dynamics.

As a developing of idea about bringing to light dominant factor, one may regard the principle of limiting factors which was first applied by Liebig (1885) to calculate concentrations of substances in chemical reactions. I.A.Poletayev used this approach when calculating rates of processes. According to the Poletayev's principle of limiting factors, at any moment intensity of the output process is limited by the least intensive component of the input process. In other words, if y is the response and x_i are the input values then

$$\frac{dy}{dt} = \min_i (f_1(x_1), f_2(x_2), \ldots, f_n(x_n)) \quad (1.8)$$

where f is a positive monotonous function which depends on the i-th environmental factor x_i. As external factors, one can usually single out physiological active radiation (PAR), CO_2, humidity, temperature of air, nutrients etc. We may note that instead of equation (1.8) a function with saturation is often applied which expresses limitation of asymptotic behaviour of the response y by large values of the factor x.

In order to gain an understanding about mechanism of growth and development of plant and its separate organs, as well as to study the environmental influences, from the beginning of the 1960-ties one has proceeded to develop complicated dynamical models reflecting in detail the concepts concerning mechanisms of productional process and the structure of plant organisms.

One of the main methods intended for modelling of tree growth is working out of balance relations. As the first balance equation, one may consider Bertalanffy's model which presents the

rate of mass change as the difference between photosynthesis and respiration (1942):

$$\dot{M} = \Phi(M, \varphi) - R(M, \varphi) \qquad (1.9)$$

where M is the mass of plant (or, perhaps, the mass of phytocenosis), Φ is the net photosynthesis, R is the loss of mass on account of respiration and fall of leaves, φ is the set of ecological parameters.

Using power functions, this equation may be written as

$$\dot{M} = a(\varphi)M^n - b(\varphi)M^m \qquad (n,m - consts) \qquad (1.10)$$

On the basis of the balance principle and supposing the energy of light being the main source of tree growth, Poletayev (1966) proposed a model describing growth and development of free-to-grow trees:

$$\dot{h} = a - bh^2 \qquad (1.11)$$

Here h is the height of tree, a,b are constants intrinsic for the given species. When working out this equation, an assumption took place about surface of tree being proportional to h^2 and mass of tree being proportional to h^3. Taking into account the energy obtained by plant, the equation (1.11) may be written in the standard form as follows

$$\dot{h} = a\frac{E}{S} - bh^2 \qquad (1.12)$$

where E is the energy, a and b are constants, S is the surface of tree.

Owing to division of plant into separate organs, the improved models of the type (1.9) include also both input and output flows. As an example, we describe the model for growth of plant (Ross, 1975) that became the basis by developing of many other models (Kull, 1986, Rachko, 1979, etc). The given model includes four equations, namely:

$$\dot{m}_J = K_F \sum_{i=1}^{4} \alpha_{ij} \varphi_{ij} - K_R R_j - V_j + M \sum_{i=1}^{4} \beta_{ij} \quad (j=\overline{1,4}) \quad (1.13)$$

describing rates of growth for leaves, stems, roots and reproductive organs respectively. In this model m_j is the mass of the respective organ, φ_j and R_j are photosynthesis and respiration of the J-th organ respectively, V_j is the dry biomass fallen away from the J-th organ during twenty-four hours. Values α_{ij} and β_{ij} form the matrices of vegetative reproductive growth, i.e. they determine distribution and redistribution of assimilates Coefficients K_F and K_R, matrices $\{\alpha_{ij}\}$ and $\{\beta_{ij}\}$, as well as character of functions φ_{ij}, R_j, V_j are defined concretely for separate stages of growth and development. Thus, model (1.13) may be characterized as a semi-experimental one since description of stages, coefficients and functions is accomplished at the experimental level.

We may note there are analogous models for describing balance between components of forest stand and environment (Oja, 1984).

By working out of the model based upon the principle of limiting factors (Λ-systems), balance equation of the type (1.13) is a piecewise linear one and can be presented as (Gilderman et al., 1970)

$$\frac{dx_i}{dt} = \sum_j (\alpha_{ij} - \beta_{ij}) P_j \quad (1.14)$$

Here α_{ij}, $\beta_{ij} > 0$ are constants corresponding to rates of the processes which proceed with intensities P_j respectively. In this case $P_j = \min_J E_j$ where E_j are external resources (in the sense mentioned above).

On the basis of the principle of Λ-systems, Poletayev (1966, 1973) worked out several models for development of plants (from the most simple models to the multicompartment ones that take into consideration influences of light and mineral sub-

stances upon growth of plants). Those models described veri-
similar behaviour of biomass and other substances participating
in the process of growth and development of plants. One can find
similar blocks within the framework of many models describing
growth of plants (Kull, Oja, 1984).

On the basis of Λ-systems, it was worked out Kudrina's
model (1973) which has not lost its significance up to now.
Within the framework of this model, the plant is divided into
two parts: roots-bole and foliage. The internal components x_j
($j=\overline{1,12}$) are glucose, oxygen, water, carbon dioxide and mineral
salts in overground and underground parts, as well as own mass
of roots and bole. There are eight external components y_i ($i=\overline{1,8}$).
They represent values proportional to density of solar energy,
to concentrations of carbon dioxide, oxygen, water available both
in the atmosphere and in the soil, as well as to concentrations
of mineral substances in the soil. Coefficients for this model
were chosen on the basis of generalized characteristics of vital
functions of plant organisms. Solution of the model was analysed
numerically with the aid of computer. It was shown that the model
could be adapted to specific plant by coefficients being pro-
perly chosen.

An attempt was made by I.A.Poletayev to construct physio-
logically grounded model of higher plant which could describe
the whole history of plant's development (from seed to seed).
That version of model included about 500 equations and was
divided into separate blocks-submodels. The processes taking place
within each of such blocks were described on the basis of avai-
lable physiological concepts, and the specific periods of time
and concentrations were valid within each block. Unfortunately,
the given work was not completed by the author.

1.3.Recently, many models have been developed with the purpose
of explaining the growth of tree on the basis of model descrip-
tion of the principal physiological processes of its functioning.
The nature of one or another model is determined in many res-
pects by some indices such as level of modelling (separate
physiological processes, entire organism or a tree within forest stand),

respective rate of processes at the given level and biomass
dividing. These issues being solved determine partly the preci-
sion of taking into account different physiological processes.
Photosynthesis and respiration are taken into consideration prac-
tically within the framework of every ecophysiological model.
The dividing' of biomass gives inevitable rise to taking
into consideration of both transport of assimilates and their
distribution. Besides that, mineral nutrition, transpiration and
influence caused by tree crown may be taken into account within
models describing tree development. The influence of cenosis
upon tree growth is to be regarded as a separate issue. The ap-
proach to modelling of plant growth which begins with model des-
cription of basic physiological processes is presented in detail
in the monograph by Thornley (1982). The similar approach is
developed in the works of Frey, Moldau, Ross, Oja, Kull from the
Estonian research school (see monograph by Bikhele et al., 1980,
review work by Oja, 1985, thesis by Kull, 1986, and, finally,
extensive work by Kulls, 1989, where there is description of basic
contemporary concepts in the field being studied). We are going
to dwell on the review of models for some important physiological
processes which determine dynamics of plant development.

One of the principal objects to be analysed is dependence of
photosynthesis on the radiation intensity, on the concentration
of carbon dioxide, on the shape of crown, etc. At this point,
functions belonging to the Michoelis-Menten type are most widely
adopted. These functions were substantially studied in the mentio-
ned monograph by Thornley. Among them, the following functions
are applied most frequently:

$$P = \alpha I, \quad I \leq I^x \qquad \qquad (1.15\text{-}a)$$

$$P = P_{max}, \quad I > I^x$$

$$P = \alpha I P_{max} / (\alpha I + P_{max}) \qquad (1.15\,b)$$

$$P = P_{max}(1-\exp(-\alpha I/P_{max})) \qquad (1.15\,c)$$

$$P = \alpha I(1 - \exp(-P_{max}/\alpha I)) \qquad (1.15d)$$

$$P = P_{max} \ln((P_{max} + \alpha I_o)/(P_{max} + \alpha I_o \exp(-\alpha I))) \qquad (1.15e)$$

where α is the initial pitch of productivity curve P, P_{max} is the asymptotic value by $I \rightarrow \infty$.

An approximate shape of the mentioned dependence is given at the Fig.2.
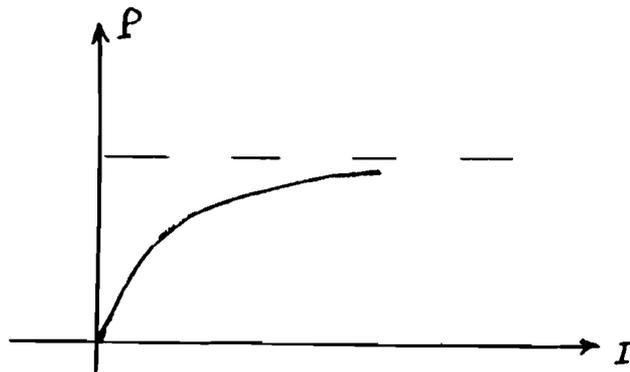
Fig.2

When passing through the plant cover, the density of light flow I may be regarded as variable changing according to the law of Lambert-Bare (proportional to the density of medium); this leads to the relation of Monsi-Saeki (Monsi, Saeki, 1953):

$$I(Z,t) = I_o \exp(-kL(Z,t)) \qquad (1.16)$$

where $I(Z,t)$ is the density of light flow at the level Z, I_o is the respective density above the tree canopy, $L(Z,t)$ is the total surface of leaves from the top of canopy to the level Z, K is a constant (coefficient of extinction).

Photosynthetic rate depends on different factors, such as temperature, concentrations of oxygen and carbon dioxide, etc. To take them into consideration, the parameters of hyperbola P(I) may be sometimes considered as variable quantities or, besides these two parameters, the third additional parameter may be introduced, and so on. Till now, it has not been developed any theory explaining influence of the mentioned characteristics

upon photosynthesis, though there are a great number of models describing photophysical, photochemical and biochemical mechanisms of photosynthesis (see review in the Kull's book, Kull, Kull, 1989).

In some works (Ross, 1975, Bugrovsky et al., 1982, 1987), dependence of productivity of plant on architectonic of leaf surface was taken into consideration. For example, in the Bugrovsky's model influence of tree crown upon productivity was chosen according to conceptions developed by Tselniker (1983), namely: every new layer of crown is formed successively, i.e. after crown in the preceding layer being closed; within each horizontal layer, illumination and photosynthesis are considered to be equal, and illumination is calculated in conformity with the law of Monsi-Saeki (1.16). Within mentioned model dependence of productivity on mass of foliage at one layer Ma and on productivity of photosynthesis KP(I) is calculated in accordance with semiempirical equation

$$\frac{dP_i}{dt} = KP(I)(M_{\wedge 1a} - K_{CT}B)_i \qquad (i = \overline{1,n}) \qquad P = \sum P_i \qquad (1.17)$$

where P_i is the photosynthetic production, $M_{\wedge 1a}$ is the mass of foliage at one layer for trees belonging to forest site 1a, B is the forest site, K_{CT} is a certain fitting factor.

Moldau equation (1971) is also a semi-empirical one; it expresses dependence of the rate of biomass increment for photosynthesizing plant divided into three organs (leaves, bole with foliage and roots) on PAR intensity, on concentration of CO_2 in the atmosphere and on quantity of water. This formula takes into account also losses of biomass by respiration and is given by (OJa, 1984)

$$y = \Delta m \frac{a \lambda_1 S_1 - a\lambda_1 \sum\limits_{i=1}^{3} \frac{S_i C_i}{\lambda_2}}{1 + a\lambda_1 S_1 \frac{b(1+\delta)}{\lambda_3} \frac{\lambda_2}{S_3}} - \sum\limits_{i=1}^{3} R_{oi} S_i \qquad (1.18)$$

Here S_i are the surfaces of leaves, bole and roots respectively, C_i and R_{oi} are the respiration factors for the mentioned organs, a,b,δ are the coefficients expressing relation between H_2O and CO_2, λ is the characteristic of PAR intensity. This formula, with some additions, was used within the framework of model for tree growth proposed by Rachko (1979) which is described below.

It should be noted such semi-empirical dependences are often submodels within the framework of long-period models of plant growth.

Many authors examined <u>respiration</u> of plants while analysing their growth. Among substantial works, we should mention models developed by Tooming, Makri and Vitt (see Thornley, 1982, Chetverikov, 1985, Oja, 1984, Kull, 1986). Chetverikov realized comparative analysis of three mentioned models and cleared up approximate limits of their applicability. At present, it's generally accepted that it is necessary to distinguish between respiration of growth, respiration of maintenance and, perhaps, respiration of transport. According to Thornley's (1982) or Markl's (1970) scheme, respiration of maintenance is always proportional to the fund of assimilates within plant whereas respiration of growth, depending on the applied scheme, may be proportional either to mass of plant or to productivity or to mass of assimilates.

When dividing biomass of modeled object into separate organs, all three types of respiration can be taken into account

for each of them. Such approach was used only in a few models known for us.

Only within few well-known ecophysiological models of tree growth, respiration of growth and respiration of maintenance are considered separately (Shugart et al., 1974, Agreen, Axelson, 1980, Rachko, 1978, Poletayev, 1973, Kull, 1986). Within many models of tree growth, respiration is supposed to be proportional to the photosynthesizing surface of tree (to be calculated on the basis of allometric relations) that may lead to essential drop in precision of calculations, especially for the longer periods.

On a level with photosynthesis and respiration, one of the major components within the model of plant growth is the submodel of transport and distribution of assimilates.

Description of the process associated with distribution of assimilates is the necessary constituent when describing plant as multiorgan system. Mechanisms describing transport and distribution of assimilates are rather debatable (Bikhele et al., 1980). That is why in a number of models only empirical curves are used as functions representing growth of individual organs. There are several methods to describe distribution of assimilates:

1. Use of empirical growth functions allowing to reveal the rate of photosynthetic products passing into certain organ at any moment of growth. As a model of growth, the balance relation of Ross (1.13) is used. An example of such approach gives the Promnitz model (Promnitz, 1975) that is described below;

2. Use of "the principle of attracting centres". According to it, assimilates move at first towards places where they are consumed most intensively (Ericsson, 1979).

3. Assumption about maintaining of certain allometric relations between tree dimensions (Poletayev, 1966, Kofman, Kuzmichov, 1981). Similar assumption was formulated by Japanese authors within the framework of their "tubular model" describing shape of plants (Shinozaki, 1979).

4. Distribution in accordance with the extremal principle. According to it, assimilates are distributed among organs so that maximum increment of plant may be ensured during the next stretch of time. The Rachko model (1979) belongs to models based upon this principle. It should be noted this optimization principle is widely applied when describing plant dynamics.

5. Distribution in accordance with principle of limiting factors (Poletayev, 1973, Kudrina, 1973, Karev, 1988). The model developed by Oja may be included in this group (1984).

6. Distribution is supposed to be proportional to mass ratio of individual organs (Bugrovsky et al., 1982, 1987). Some properties of such models are considered above (see formula (1.18)).

7. If several funds of assimilates are considered within a model, a natural opportunity offers to accept movement between funds to be proportional to difference between their values. Such approach was used by Thornley (1982), as well as in a number of other plant models (Bikhele et al., 1980).

We can note that physico-chemical mechanism of distribution is not discussed within majority of mentioned models. One of hypotheses describing such mechanism is given by the model PUU-1 (Kull, 1986). Within this model (according to Münch principle), the movement of assimilates all over phloem is supposed to take place as a mass flow. In the capacity of motive force for this flow, one may regard potential difference of pressure in different parts of phloem associated with difference of components of water potential in these organs. Distribution of assimilates being explained from the points of view 5.-7. leads to the analysis of relations between growth rates and relative dimensions of plant organs. The generally accepted point of view consists in suggestion about increase of sizes of the organ "being in need". Oja (1986) investigated a question concerning relation between growth of both over-and underground parts of plant and distribution of assimilates, and obtained similar results.

It should be noted dividing of biomass and compartmentation when modelling may be chosen in different ways, depending on modelling purposes. There are models with undivided biomass (organs), for example, models by Poletayev (1966, 1979), as well as many models with dividing into two parts (Poletayev, 1973, Oja, 1985, etc.), and, finally, some models involving process of dividing into three or four parts (Promnitz, 1975, Thornley, 1976, Kull, 1986, Karev, 1988 etc.).

It should also be noted that some essential physiological processes, such as mortality, nitrogen exchange, etc., are taken into consideration in a number of models. One more factor affecting the process of plant growth (and taken sometimes into account within models) is <u>the water exchange in conjunction with passing of mineral elements</u>.

Provision of different organs of tree with water is usually characterized by potential Ψ , and its gradient is regarded as force transfering water to the separate organs. Within a number of models (Rachko, 1978, Poletayev, 1966, 1973), water exchange doesn't acquire concrete expression. Within the framework of more detailed models (Thornley, 1982, Kull, 1986), the description of block corresponding to water exchange was included into the respective model.

1.4. And now we go on to the description of some models which display the foregoing principles of model construction.

Within the framework of Promnitz model (Promnitz, 1975), plant is divided into three parts, namely leaves, roots and stems. As for stems, one distinguishes height increment and thickness increment. Respiration intensities for each organ $R_i(t)$ and photosynthetic rate $P(t)$ are included into this model.

The model presents a system of four differential equations

$$y_i = L_i(t)P(t)y_i(t) - R_i(t) \qquad (1.19)$$

where L_i is the portion of assimilates sent to the respective organ. After the example of Thornley (1970), one distinguishes between respiration of growth and respiration of maintenance within the framework of the given model. Distribution of assimilates is supposed to conform to the experimental function.

Within the Oja model (1985, 1986), the investigated question consists in distribution of assimilates between over-and underground parts of plant (tree) during sufficiently long period of time (this specific period depends on the plant species involved). The model has a natural form:

$$\begin{cases} \dot{B}_S = g_S(e\varphi - R_{os}) \\ \\ \dot{B}_R = g_R((1-e)\varphi - R_{or}) \end{cases} \qquad (1.20)$$

where B_S and B_R are masses of over-and underground parts of plant respectively, φ is the total photosynthetic productivity, R_{os} and R_{OR} are losses caused by respiration of over-and underground parts respectively. In this model, $e = e_S$ is the portion of assimilates in the overground part of plant, $e_R = 1 - e_S$ is the respective portion in the underground part. Photosynthesis is given by

$$\varphi = \omega S_m B_{oi}(B_S^x)^{1-\alpha_S}$$

It is considered that dependence of photosynthesis and respiration on masses of over-and underground parts of plant can be expressed by means of power function. Besides that, photosynthesis is proportional to the value which corresponds to the provision of leaves with water. According to the principle of limiting factors, this value is expressed by

$$\omega = \begin{cases} 1, & \text{if } RB_R \geqslant \sqrt{B}_S \\ RB_R/\sqrt{B}_S, & \text{if } RB_R < \sqrt{B}_S \end{cases}$$

where R is the coefficient of proportionality.

In the works by OJa, the following hypotheses about distri-
bution of assimilates were verified: 1/ prevailing utilization
in leaves; 2/ competitive distribution; 3/ distribution accor-
ding to requirement; 4/ distribution inversely proportional to the
activity of respective organ. Depending on the age of plants,
the first or the fourth hypothesis is turned out to be correct.

Within the framework of Bugrovsky's model (1987), the
photosynthetic productivity was taken into account by means of
formula (1.17), and the increment of biomass was given by

$$
\left\{
\begin{array}{l}
\dfrac{dM}{dt} = P - D - M_m \\[2ex]
\dfrac{dP}{dt} = K_D M.
\end{array}
\right.
\qquad\qquad
\dfrac{dM_m}{dt} = K_m M
\qquad\qquad (1.21)
$$

Here M is the total mass of forest stand, D is the loss due to
respiration, M_m is the mortality coupled with fall of foliage,
K_D and K_m are the coefficients associated with rates of the
processes mentioned.

Distribution of newly arising mass is assumed as follows:

$$ dM = dM_\Lambda + dM_c + dM_b $$

$$
dM_\Lambda = \left\{
\begin{array}{ll}
dM\dfrac{M_\Lambda}{M_c + M_b}, & \text{if } I_i > I_n \\[2ex]
0, & \text{if } I_i \leq I_n
\end{array}
\right.
$$

Here M_Λ is the mass of leaves, $M_c + M_b$ is the mass of nonphoto-
synthetic parts, I_n is the PAR intensity which corresponds to
the compensation point at the photosynthetic curve, n is the
number of foliage layers.

Within this model, the dependence of forest stand produc-
tivity on climatic conditions is retraced. (It should be noted
that difference between single-growing tree and forest stand is

not manifested within the framework of this model). Thus, the annual productivity is given by the following product:

$$P = P_{max} K_a K_T K_w$$

where P_{max} is the maximum annual productivity under tropical conditions, K_a, K_T, K_w are the coefficients determined by duration of vegetation period, by temperature conditions and by water conditions respectively. Taking into account dependence of mentioned coefficients on duration of vegetation period G, on mean temperature T, on the temperature T_{on} which is optimal for photosynthesis, as well as on precipitation amount W, on required precipitation amount W_n, on maximum W_{max} and minimum W_{min} (when photosynthesis is considered to be equal to zero) precipitation amount, the dependence of productivity P on all the mentioned factors is obtained:

$$P = \begin{cases} P_{max}\dfrac{G}{12}\dfrac{T}{T_{on}} \sin \dfrac{(W-W_{min})}{2(W_n-W_{min})} \\[4pt] \text{by } 0 \leqslant T \leqslant T_{on} \qquad W_{min} \leqslant W \leqslant W_{max}; \\[8pt] P_{max}\dfrac{G}{12}\left(2-\dfrac{T}{T_{on}}\right) \sin \dfrac{(W-W_{min})}{2(W_n-W_{min})} \\[4pt] \text{by } T_{on} \leqslant T \leqslant 2T_{on} \qquad W_{min} \leqslant W \leqslant W_{max}; \\[8pt] 0, \text{ by } T < 0, \quad T > 2T_{on}, \\[2pt] W < W_{min}, \quad W > W_{max} \end{cases} \qquad (1.22)$$

This model has been identified for different regions of Ubsu-Nur valley and prepared for computer calculations. As for taking into consideration climatic influences, it's obvious that this model may be regarded as simulated (or "fitting") one. Considerations concerning tree development (that are included into the model) seem to be rather substantial.

Having developed Poletayev's model (1973), Karev presented four-compartment model (1988) which represented mathematical

synthesis of two blocks, namely: physiological concepts about mechanism of tree growth (presented with the aid of model developed on the basis of principle of limiting factors) and equation of tree growth that was worked out proceeding from allometric dependence between increment of tree biomass and height of tree. The model contains such variables: cambium m_1, active biomass m_2, carbohydrates m_3, wood (non-active biomass) m_4, height of tree H. It is given by

$$
\begin{cases}
\dot{m}_1 = A_0 m_1 \min(1, B_1 Z) - A_1 m_1 - a_1 m_1 \\
\dot{m}_2 = A_1 m_1 - A_2 m_2 - a_2 m_2 \\
\dot{m}_3 = P - B_1 m_1 - B_2 m_2 H - A_0 m_1 \min(1, B_3 Z) \\
\dot{m}_4 = A_2 m_2 + a_1 m_1 + a_2 m_2
\end{cases}
\tag{1.23}
$$

Here A_i, a_i, B_i are the intensities for transition of one kind of biomass into another one. Within this model, it is supposed that assimilates are mainly consumed for principal exchange and transport, whereas their consumption for tree growth is proportional to the demands of this process and to the relative provision of assimilation which amounts to $Z = m_3/S$, where S is the rate of the mentioned consumption necessary for reaction to proceed without any limitations: $S = B_1 m_1 + B_2 m_2 + B_3 (m_1 + m_2)$. System (1.23) may be closed proceeding from allometric considerations, namely $H = m_4^{1/3}$, or by means of obtaining an equation for H which is similar to equation (1.11). In the most simple case

$$
H = A_1 m_1 / \pi B^2 H^2
\tag{1.24}
$$

Equations (1.23)-(1.24) make up a closed system. The photosynthetic rate P which appears in this system can be expressed through the speed of light energy obtained by tree according to formulae (1.15) or through another way known from the literature.

Among models by which an attempt was made to retrace growth and development of tree on the basis of ecophysiological considerations, we may mention two so-called "large models" intended for description of both short-periodical and long processes. The question is about Rachko's model (1979) and Kull's model (1986).   Both models are detailed and consist of separate blocks. In some cases, these models describe one or another process influencing the growth in a similar way. However, it should be noted there is a significant difference between them While Rachko's model belongs to optimization models (i.e. distribution of vital activity products is assumed to maximize process of biomass increment), Kull's model interprets this problem from the point of view of Münch's principle (distribution is actually determined by potential difference of water along the conducting tracts). It should be noted that, unfortunately, the detailed comparison of results obtained in both models ("growth trajectories") has not been accomplished.

After the example of G.Thornley and H.Moldau, within Rachko's model one discerns three organs, namely leaves, bole and roots. Mechanism of biomass growth which is included into this model consists of the following. New biomass is generated in the process of photosynthesis, and the photosynthetic rate depends on the following parameters: PAR, supplies of accessible water, concentration of carbon dioxide, air temperature. Growth depends also on the level of nitrogen, phosphorus, calcium and sodium which are accessible for tree.
Distribution of assimilates corresponds to the principle of maximum productivity (on condition that environment remains unchanged). Biomass increment is only affected by mineral element with minimum content. Supply of mineral elements is affected by both reproduction and foliage fall during vegetation period. From the mathematical point of view, this model represents the system of balance equations (describing circulation of nutrient elements) supplemented by equation of productivity rate and by equation expressing relationship between values of biomass for different parts of tree and their geometrical structure. Thus, the total system is expressed by

$$X_i(t+\tau) = X_i(t) + l_i(t)\tilde{y}[X_J(t), \lambda_k(t)] \times$$

$$\times [1 - \omega_i u(t)] \qquad\qquad (1.25)$$

$$Z_1(t+\tau) = Z_1(t) + X_1(t-S_1)\omega_1 P_{1i} u(t) + X_3(t-\delta_1)\omega_3 \times$$

$$\times P_{31} u(t) - \tilde{y}[X_J(t), \lambda_k(t)]\tau \cdot q_l - \varepsilon Z_1(t)u(t)$$

$$t = m\tau; \quad m = \overline{1,N}; \quad i = \overline{1,3}; \quad l = \overline{1,4}; \quad k = \overline{1,4}$$

Here X_i is the biomass of leaves, bole and roots respectively;

Z_1 is the biomass of elements N,P,Ca,Na respectively;

τ is the time delay concerning emergence of the respective substance;

$\lambda_k(t)$ are the parameters of environment, namely: PAR, H_2O, CO_2, temperature;

$\omega_i, \delta_1, \varepsilon$ are the parameters concerning circulation of nutrients, namely: portion of mortality for the i-th organ during vegetation period, time needed for 1-th mineral element to return into the circulation process, portion of substances which abandoned the circulation process (these parameters are conside red to be given beforehand);

P_{i1} is the content of 1-th nutrient in i-th organ;

q_1 is the content of 1-th nutrient in the new biomass;

$$u(t) = \begin{cases} 0, & \text{if } t \neq n(n_1\tau) \\ 1, & \text{if } t = n(n_1\tau) \end{cases}, \quad n=1,2,\ldots$$

where $n_1\tau$ is the duration of vegetation period;
portions of biomass distributed between organs of plant are determined according to the law of maximum productivity:

$$l_J(t) \, y(t+\tau) = \max y_1\{x_J(t) \, l_J(t),$$
$$y(x_J(t), \bar{\lambda})\tau, \bar{\lambda}(\tau)\} \qquad\qquad (1.26)$$

$$J = \overline{1,3}; \quad \Sigma l_J = 1; \quad l_J \geqslant 0$$

where (in accordance with Liebig's principle) $y_i = \min\{y(t), Z_1(t)/q_{1l}\}$, and function $y(t)$ is the law for generating of

new biomass (it is defined by formula (1.18)), and, practically speaking, is calculated as difference between photosynthesis and respiration. Within this model, dependences on amount of water in root system, on concentration of carbon dioxide in atmosphere, as well as on temperature (Van-Hoff's law) are introduced into photosynthesis. Values S_i which appear in the formula (1.18) and are equal to surfaces of respective organs can be expressed through biomass as follows

$$
\left\{
\begin{array}{l}
S_1 = \alpha X_1 \\[2mm]
S_2 = (\sigma \pi)^{1/3} (4 X_2 / A)^{2/3} \\[2mm]
S_3 = 4 X_3 / d \rho_2 \\[2mm]
Z = (K_3 X_2)^{1/3}, \quad K_3 = 4 \delta^2 / \pi \rho_1
\end{array}
\right.
\qquad (1.27)
$$

where α, δ, d are the average constants of the tree being modeled (they depend on the surrounding forest stand); ρ_1, ρ_2 are the specific gravities of bole and roots respectively. And, finally, if the initial conditions

$$
X_i(0) = X_i^0 \qquad (\overline{i=1,3})
$$

$$
Z_1(0) = Z_1^0, \ldots, Z_1(N \cdot n_1 \tau) = Z_1^{N_1} \qquad (\overline{i=1,4}) \qquad (1.28)
$$

are given, the whole complex of equations (1.18),(1.25),(1.28) permits to describe Rachko's model completely.

The model being considered permits to carry out analysis of growth (forecast) for the period of several years. An attempt to take into account processes of different scale within the framework of only one model makes it very complicated. Solution may be found only with the aid of computer calculations, and the applied optimization procedure makes this search very time--consuming. The given model is almost beyond analytical analysis (it is possible only to analyse pre-conditions put into this model), and it is not sufficiently identified.

At present, Kull's model PUU-1 (1986) is one of the most complete ecophysiological models of tree. It desoribes satisfactorily the dynamics of growth and development for short and long periods of time without introducing any additional hypotheses (such as optimizing one) but proceeding only from the author's conceptions about biochemical mechanism of the processes involved. Within this model, all processes are described by balance equations (the way it is done in the model of Ross) by which, however, functions are given not empirically but through mechanisms, i.e. on the basis of equations included into the model.

Four organs are discerned within this model, namely leaves, bole and branches, thick roots and thin roots, with the respective masses W_L, W_S, W_K, W_R. It's considered there are three funds of assimilates located in leaves, bole and roots respectively (with the corresponding masses C_L, C_S and C_R). On a level with W and C, fund of nitrogen compounds N and height of tree H are regarded as model variables. The basic balance equation is given by

$$\frac{dW}{dt} = P+Q-R-V \qquad (1.29)$$

where P is the photosynthesis, Q is the nutrition, R is the respiration and, finally, V is the fall of foliage. By means of writing out of equation (1.31) for separate organs, the system of differential equations may be worked out which contains blocks referring to photosynthesis, transport and distribution of assimilates, water exchange, nitrogen exchange, respiration, fall of foliage, growth respectively.

Within this model, photosynthesis is considered to be proportional to illumination f(I) and to moisture supply $1+b_p\Psi_L$ (Ψ_L is the water potential in leaves), as well as to be dependent on temperature (the latter dependence is assumed to be described as step function because it's considered that photosynthesis, as it is supposed in Rachko's model, proceeds equally within a certain temperature range whereas the given process

doesn't take place beyond this range). Within Kull's model, the
block of photosynthesis is similar to the corresponding block
described within Rachko's model. The dependence of photosynthesis
on illumination is accepted to be hyperbolic one (in accordance
with formula (1.15b)) while the illumination may be expressed
in compliance with the relation of Monsi-Saeki (1.16). Thus[x],

$$P = P_o W_L f_p(I)(1+b_p+\psi_L)f(I(t)) \qquad (1.30)$$

where P_o is the specific photosynthesis under optimum condi-
tions,
$$f_p(T) = \begin{cases} 1, & T > 0 \\ 0, & T \leq 0 \end{cases}$$

Within the given model, mineral nutrition is reduced to
nitrogen one. Assimilation is considered to be proportional both
to quantity of nitrogen in soil and to concentration of carbohyd-
rate assimilates which accompany nitrogen while it moves.

Respiration of organ, as well as of the whole plant, is
divided into three components corresponding to growth, transport
and maintenance. The first component is proportional to growth
rate whereas two last components are supposed to be proportional
to amount of assimilates. By this approach, the maintenance
depends essentially on temperature (here this dependence is
regarded as linear one). For each organ respiration is conside-
red separately.

Fall of foliage and roots is supposed to be proportional
to their mass. Within Kull's model, transport of assimilates is
considered to conform to the law of Münch, namely it is directly
proportional to the motive force (which is the sum of potential
differences of water and carbohydrates both within conducting

---

[x] It's obvious that it would be more correct to consider
$P = \min(\alpha f(I(t)), 1+b_p \psi_L)$. Otherwise, it might occur deficiency
of illumination could be compensated owing to water potential.

tract and beyond it) and is inversely proportional to the resis-
tance met along the movement tract (it can be expressed through
the surfaces of respective organs and through the specific
values). It turned out this model allowed to describe mechanisms
of ascending and descending flows. Direction of movement of assi-
milates being changed is of great importance for broad -
- leaved trees , whereas in case of evergreen plants direc-
tion of transport of assimilates is practically always descen-
ding one.

This model contains 9 equations and 40 dependences (used
for determining of equations). It is perfectly well identified
for spruce and, probably, may be fit to simulate process of
growth for other species.

Such a detailed model may be used to analyse influence of
various outside reagents upon growth and development of trees.

1.5. To sum up the results concerning consideration of
principles used for modelling of separate tree, we may note the
following (Kull, Kull, 1989).

The history of ecophysiological modelling of processes
taking place in trees may be divided into three stages. To the
models developed at the first stage and originated from the
logistical model (1.8) one should refer Bertalanffy equation, as
well as its various modifications, for instance Robertson equation.
To this group one should also refer more improved models by
which the system of flows becomes complicated owing to dividing
of plant into separate organs. To such models one may refer, for
example, model of Ross (1.13) which represents balance relation
by empirical selection of functions. Arising of classical works
on modelling of productivity process (law of Monsi-Saeki (1.16))
was associated with this stage.

Models of the second generation are characterized by detai-
led description of photosynthetic block and the processes taking
place within plant cover. Owing to this peculiarity, such models
are often very bulky. While describing subblocks, empirical
functions are quite often applied. It should be noted at this
stage the models of plant are considered without concrete defini-

tion of species (Poletayev, 1973, Kudrina, 1973) rather often. As an important step taken within this stage, one may mention introducing of compartments(Thornley, 1980), as well as taking into account the meaning of mineral substances and water exchange. Arising of classical principles of modelling (Poletayev, 1970) refers also to the given stage. Rachko's model may be also referred to models of the second generation.

Within models of the third generation (models of Kull (1986) and Karev (1988) belong to it), process of growth is of great importance because it's considered as regulator of process concerning distribution of viability products. Giving up growth, as well as model description of process associated with distribution of viability products are very essential. Within these models, the optimization principle is applied to a less degree, but functioning turns out similar to the optimal one (Kull, 1986). It is not unlikely to suppose that unfinished Poletayev's model was guided by the principles developed within the given class of models.

The classification being presented is, of course, very relative. When modelling tree within forest stand or by modelling age dynamics of tree population, an approach combining simple models of growth for one tree with model description of change in numbers of forest stand trees and change of competition mechanism proves to be very promising. It should be also mentioned about particular models of separate processes which can be useful for solving some problems associated with growth and development of plants.

2. Models of dynamics for forest stands

2.1. Processes described by the models examined above are the separate components within development of forest stand as a whole. As one more component, the model of influence of the association upon growth and development of the individual should be considered. Primarily, modelling of forest stand, as well as modelling of separate individual, was based upon empirical models describing dependence of stand characteristics (num-

ber of trees, total mass of forest stand, total area of boles, etc.) on time. Such dependences have been widely applied in forestry to describe approximately dynamics of even-aged stands composed of trees belonging to only one species. In this case, self-thinning is regarded as a principal process. Therefore, many formulae have been suggested to describe this process (see reviews, as well as Oja, 1985, Sholokhov et al., 1990). Numbers of trees in forest stand may be associated with stand age, diameter and height of trees, as well as with some physiological indices. Review of such models is presented in the monograph by Terskov and Terskova (1980) who also propose own different formulae to describe self-thinning at separate stages of stand development. There is a widespread formula of self-thinning in accordance with the so-called law of "3/2", namely

$$b = a_s N^{-b} \qquad (b = 3/2) \qquad (2.1)$$

and it represents allometric relation between the total biomass of forest stans b and the number of boles N (a_s is the constant dependent on the given tree spacies). Applicability of a allometry by describing of forest stands (as well as by describing of one separate tree) is investigated in detail in works by Kofman (1981), as well as by Kofman, Kuzmichev, Khlebopros (1979).

The investigation of interaction between neighbouring trees is very essential for understanding of stand dynamics. One describes usually influence of competition upon growth of trees in stand and upon their number. (There are also some observations concerning allelopathic relation between individuals being members of forest stand. However, the respective models were not discovered (Oja, 1984)). Plenty of models have been proposed to take into account the existing competition. Within the most simple models, the mutual competitive influence is taken into consideration mainly with the aid of the so-called competition indices. Most of such indices are based upon taking into account the limitation of leaf area within the forest stand. Measure of deficiency is expressed through the relation between accessible and required areas (or, in a three-dimensional case, spaces) of growth.

The latter area is usually called "nutrition area" and defined as convex polygon with dimensions which are functions of linear parameters of the considered tree and its neighbours (for example, diameter or height) or functions of crown dimensions. The accessible area is found by means of dividing of forest canopy into "nutrition areas" of trees. The polygonal models were analysed by Plotnikov (1979). System for modelling of "nutrition areas" and selection of optimum areas were developed by Shvidenko and Yuditsky (Shvidenko, 1981).

The second type of competition indices is based upon taking into account the overlapping growth zones (influence zones) of tree within a forest stand. The more is the overlapping of growth zones at the map of forest stand, the more is the competition. Such competition models were analysed by McMurtrie(1981).

Furthermore, there are indices calculated according to distances from neighbouring trees by taking into account their diameters. Other indices are based upon calculation of the angle formed by bole of the competing tree (the idea about relascopic forest estimation is used, etc.). The mentioned methods don't specify more exactly which of resources defines competition.

It's obvious the above-stated models are not ecophysiological (or, more precisely, explaining) ones. They establish only certain dependences and may be useful in forestry since they take into account biometric indices which are determined easily by observations.

2.2. As more promising, one may regard description of temporal dynamics concerning number of trees, as well as mutual influence of number of trees and variables defining structure of trees (mass, height, etc.). Model of association dynamics is to include analysis of competitive interactions regarded as most essential within association.

Generally, model of dynamics of even-aged association may be presented by

$$
\left\{
\begin{array}{l}
\dot{X} = F(t,x,l,g(t)) \\[2ex]
\dfrac{\partial l}{\partial t} + \mathrm{div}(lF) = -\mu l \\[2ex]
g(t) = \displaystyle\int u(x)\, l(t,x)\, dx \\[2ex]
l(0,x) = \varphi(x)
\end{array}
\right.
\qquad (2.2)
$$

Here $X(X_1,\ldots,X_n)$ is the set of variables describing an individual plant, $l(t,x)$ is the population density, $\varphi(x)$ is the initial distribution of densities of individuals within association, μ is the mortality rate, $g(t)$ is used for calculation of the external resource corresponding to individual plant (for example, by $u(x)=1$ the given function is equal to total population numbers) and, thus, describes the process of competition.

Note. Within many models (for example, Gurtin-MakCamy, 1977), it's supposed the mortality rate μ may depend on the total population volume (on values which are similar to $g(t)$) in nonlinear way. This permits to take into account, at the phenomenological level, increase of mortality resulted from resource shortage while excessive growing of the population density.

Thus, the first equation determines the growth law for an individual plant by taking into account competition as external resource, while the second one is the balance equation.

Within many models, balance relations being similar to Bertalanffy's equation (1.9) (perhaps, in the incremental form) are used as the first equation of the system (2.2). As examples of such models, we can mention equations associated with diameter of plant or with its height (Poletayev's equation (1.11)).

The second equation of the scheme (2.2) may be presented, in the most simple case, by

$$
\dot{N} = -NG(E,t) \qquad (2.3)
$$

where $G(E,t)$ is the mortality rate, N is the number of trees, E is the external resource.

At present, it is accepted to distinguish density-dependent β and density-independent α components of the function $G(E,t)$ (Semevsky, Semenov, 1981, Korzukhin, 1986). Then the equation (2.3) may be presented as

$$N = -(1 - \alpha\beta(E))N \qquad (2.4)$$

or

$$N(t+1) = \alpha\beta(E)N \qquad (2.5)$$

Models which are similar to (2.3)-(2.5) are used by many authors. We may note, in particular, one of the Shugart's models (Shugart, 1984), namely

$$\begin{cases} D_i = a(\varphi) \left[f(D_i) - g(D_i) \right] \\ \\ N_i = -\mu(D_i)N_i \end{cases} \qquad (i = \overline{1,n}) \qquad (2.6)$$

where D_i is the diameter, N_i is the numbers of the i-th cohort (group of even-aged plants), φ are the ecological parameters, in particular, resources consumed by photosynthesis (among them, light and water depend on numbers of the whole system), λ is the mortality coefficient. This model was applied by the author to construct large-scale simulation model for investigation of forest dynamics. Within this model, a,f,g are empirical functions describing accumulation and expenditure of organic matter, mortality depends on density (through D_1 in an indirect way), namely: $\mu = \mu_1$ if $D_i \geqslant D_1 \min$, and $\mu = \mu_2$ if $D_i < D_1 \min$ (threshhold dependence), $\mu_1 < \mu_2$; n is the number of species within population.

Description of competitive interdependences within the population proves to be most complicated. To be more precise, this problem consists in the calculation of amounts of limited

resource corresponding to one individual. Depending on this re-
source, the population productivity is usually described by hy-
perbolic function both in analytical and simulation models (Mol-
dau, 1984, Bikhele et al., 1980, Tooming, 1977, Shugart, 1984,
etc).

And now we dwell on the questions of competition at greater
length. In opinion of the most researchers, competing for light
proves to be the most essential component. We distinguish three
models which refer to this type competition.

1. Model of competing for light ("turbid layer").

In this case, density of the light flow at the level Z is
supposed to be calculated according to the law of Monsi-Saeki
(1.16).

Function $L(Z,t)$ depends essentially on the conditional
shape of crown and may be presented as follows:

$$L(Z,t) = \int_{o}^{Z} S(H,Z)N(H,t)dH \qquad (2.7)$$

Here $N(H,t)$ is the density of trees in the population which are
characterized by height value H at the moment t, $S(H,Z)$ is the
value of leaf area from the top H to the level Z which can be
expressed through the density of leaf area distribution for the
tree with height H at the level Z: $S(H,Z) = \int_{Z}^{H}S(H,u)du$. It's
function $S(H,Z)$ that can be used to model different forms of leaf
area. For example, by $S(H,Z) = \sigma H$ the tree may be modeled with
the aid of rectangle, whereas triangle with its base situated
above or below may be a model when $S(H,Z) = 2\sigma Z$ or $S(H,Z) = 2\sigma(H-Z)$
respectively (σ = const).

Photosynthetic productivity $P(t,N,H)$ may be calculated
through the density of light flow: $P = f(I)$, where function f is
taken from the formulae (1.15). Let $P_o(H)$ be the photosynthetic
rate for free-to-grow single tree. Then the relative photosynthe-
sis is given by

$$\Phi(t,N,H) = P(t,N,H)/P_o(H) \qquad (2.8)$$

Thus, the equation describing dynamics of the structural variable (height H) for a tree growing within even-aged forest stand may be expressed by

$$\dot{H} = a\Phi(t,N,H) - bH^2 \qquad (2.9)$$

For instance, by any distribution of crown by height, the photosynthetic rate for "population of identical trees" is given by

$$\Phi(t,N,H) = \alpha I_o(1-\exp(-KNH^2))/KH^2N \qquad (2.10)$$

on condition that function f is chosen in accordance with (1.15a). If $N \to 0$ (free-to-grow tree), $\Phi(t,N,H) \to \alpha I_o$, and equation (2.9) coincides with Poletayev's equation (1.12).

To describe a multistoried stand, formula (2.7) is to be generalized, namely

$$L(Z,t) = \sum_{i=1}^{m} N_i(H_i,t)S(H_i,Z) \qquad (2.11)$$

where $N_i(H_i,t)$ and $S(H_i,Z)$ are repsectively the density of tree number and the leaf area trees within the i-th storey. The model of multistoried stand may be presented as

$$\dot{H}_i = a_i\Phi_i(t,N_i,H_i) - b_iH_i^2 \qquad (2.12)$$

Here $\Phi_i(t,N,H)$ is the relative photosynthetic rate for trees of the height H_i.

Similar to the stated above,

$$\Phi_i(t,N,H_i) = P_i(t,N,H_i)/P_i(t,0,H_i) \qquad (2.13)$$

where

$$P_i(t,N,H_i) = \int_o^{H_i} S_i(H_i,Z)f_i(I(Z,t))dZ \qquad (2.14)$$

Here H_i, N_i, $S_i(H,Z)$ are the respective characteristics of trees within the i-th layer.

The model similar to (2.12) may be also worked out for stands consisting of many species. However, the difference is that coefficients a, b, as well as functions $S(H_i,Z)$ (which describes crown shape) and f (describing relation between productivity and density of light flow) may depend on number of one or another species and on number of storey.

It should be noted now that as functions describing dependence of tree numbers on time or on height of trees the following relations have been considered: Didkovsky's formula $N = N_9 \exp(-KH)$, Hilmi's formula $N = K/H^2$, Kajanus' formula $N = (K_1 + K_2 t)/t^2$, etc. The models were identified in accordance with yield tables for all versions.

To specify relations between getting stands thin and growth of trees, it was suggested to consider models combining equations of the type (2.9) or (2.12) with dynamical equation of the type (2.3) which concerns number of trees.

In case of forest stand composed of n species, the model will include 2n equations

$$\begin{cases} \dot{H}_i = a_i \Phi_i(t,N,H) - b_i H_i^2 \\ \\ \dot{N}_i = -(1 - \alpha(\Phi_i(t,N,H)^{d_i})N_i \end{cases} \qquad (2.15)$$

where, similar to above-stated, functions Φ_i and P_i are expressed according to formulae (2.13) and (2.14).

This model may be applied to describe in detail multistoried forest stand with different species, and it may be also a basis of well grounded analytical simulation model of the type (2.6) with results to be compared with observations of stand and to be investigated in analytical and numerical ways.

Karev (1985) suggested one more view on the models of the type (2.12). Having taken into account that, through transition to $n \rightarrow \infty$ in formula (2.14), the growth equation (2.12) might be written for every separate tree, the author, on the basis of mathematical methods which are not typical for the given field (theorem of Khinchin-Molchanov), could replace the system (2.12) - (2.14) by the system of two equations.

$$\begin{cases} \dot{H} = \frac{a}{H^2} \int_0^H S(H,Z) \exp(-\bar{N}\bar{S}(H,Z)) dZ - bH^2 \\ \bar{S}(\bar{H},Z) = \frac{1}{\bar{H}} \int_0^\infty (\exp(-\frac{X}{\bar{H}}) \int_Z^X S(x,y) dy) dx \end{cases} \qquad (2.15^1)$$

($\bar{H}$ is the average height, N is the numbers of forest stand) which made it possible to calculate growth of individual trees depending on their initial height, as well as on dynamics of average heights only and on number of trees within forest stand (this peculiarity facilitated also comparing of the obtained results with the observation data).

2. Model of "screens"

In the work by Korzukhin and Ter-Mikhaelyan (1982), as well as in a number of simulation models (JABOWA, FOREST, etc.), forest stand is simulated by means of the system of screens (which may be horizontal of any shape or right-angled in shape located vertically and distributed by height in an arbitrary way) necessary to calculate amount of light radiation accessible to a separate tree within forest stand. These screens are supposed to be infinitely thin, flat, not reflecting light and located paral-led to each other. The number of screens within the given surface is distributed in accordance with Poisson law with the mean value μ. Then, in case of system of horizontal screens of the same area located within the unit section, intensity of energy brought to a screen at the height h is given by

$$I(h) = I_0 \sin \varphi \exp(-\mu \, \gamma n(h)) \qquad (2.16)$$

where n(h) is the number of screens located at higher levels than the height h, γ is the coefficient of light absorption, φ is the angle of light incidence[*].

In case of system of vertical screens, let the height h be a stochastic value with the probability density P(h), and σ(h) be the width of screen of the height h. Then

$$I(h) = I_0 \, \sigma(h) \, \cos\varphi \int_0^R \exp\left(-\frac{h\gamma}{tg\varphi} \int_\varphi^\infty (Z-U) \cdot \right.$$

$$\left. \cdot \, \sigma(Z)P(Z)dZ\right)dU \qquad (2.17)$$

In particular, for population of identical screens characterized by the area S[**] we have

$$I = \frac{I_0 \, \sin\varphi}{\gamma}(1-\exp(-\gamma nS/tg\,\varphi)) \qquad (2.18)$$

While calculating photosynthetic productivity, the dependence of the type (1.15) or a hyperbolic function may be chosen. The latter is given by

$$P = \frac{r_1 E}{1+r_2 E} \qquad (r_1, r_2 - consts) \qquad (2.19)$$

Such dependence was used within a number of models developed by Korzukhin et al. Here we dwell at length on one of these models (Korzukhin, 1986). In case of even-aged population competing for only one resource, this model may be expressed as

$$\begin{cases} \dot{m} = P-q(m) \\ \dot{N} = -[1-a(w)C(Z)]N \end{cases} \qquad (2.20)$$

[*]This formula coincides (to within designations) with energy calculated in accordance with the law of Monsi-Saeki.

[**]Formula (2.18) differs only for its designations from the formula obtained on the basis of the model of "turbid layer" despite the cardinal difference of models.

Here P is presented by formula (2.19) with coefficient $r_1 = r_1(\mathcal{P}(S_L))$ being dependent on specific photosynthetic efficiency $\mathcal{P}(S_L)$,

$E = E(S_L, N)$ is the average limited resource corresponding to one individual (it is calculated by means of (2.16) or (2.18) and dependent on $S_L^{\partial\Phi}$, $S_L^{\partial\Phi}$ is the leaf area participating actively in photosynthetic process: $S_L^{\partial\Phi} = S_L \psi(S_L)$ where S_L is the total leaf area of one tree, $\psi(S_L)$ is the coefficient taking into account efficiency of interaction between leaves, N is the density of trees within given plot. Functions a and Z are density-independent and density-dependent components of survival respectively; their arguments are W and Z, i.e. normalized photosynthesis of an individual beyond population and within it.

Assuming, for allometric reasons, that

$$a \approx W^{\alpha_1}; \quad c \approx Z^{\alpha_2}; \quad q \approx m^{\alpha_3}; \quad \mathcal{P} \approx S_L^{\alpha_4}; \quad \psi \approx S_L^{\alpha_5},$$

a system may be obtained which allows to describe dynamics of even-aged association in the presence of competition for one resource. Within the mentioned work, a particular case of the model (2.20) is investigated in detail. In this case, we have linear dependence $\mathcal{P}(E)$, density-independent mortality being constant, power dependence of density-dependent mortality on its argument Z, as well as similar dependences of expenditure q(m) on mass m, mass m on diameter d, leaf area S_L (as well as specific photosynthesis $\mathcal{P}(S_L)$ and resource $\psi(S_L)$) on area of leaves $S_L^{\partial\Phi}$. As a result, the following system is obtained:

$$\dot{d} = r_s d_e^{r_4} \exp(-r_7 d^{r_2})^N - r_5 d^{r_6}$$

$$\dot{N} = -[1 - \exp(-r_1 r_7 d^{r_2 N})] N \qquad (2.21)$$

Coefficients of this system are selected proceeding from silvicultural data. This model permits to describe satisfactorily the quality dynamics of basic variables of even-aged tree population. Owing to this model, it turned out well to obtain effect of tightening of population numbers for long periods of time (irrespective of the initial density).

Similar approach was realized by Korzukhin (1985, 1987) for many other models.

3. Competing for area of growth

Ecophysiological approach to analysing of this type of competition which generalizes conceptions developed in numerous index models is presented by analytical simulation model by Galitsky and Komarov (1978), Galitsky 1990. As principal equation within this model, one considers equation for growth of tree biomass

$$\dot{m} = \varkappa \left(\frac{m_{max}}{\tau} + \dot{m}_f \right) - \frac{m_{max}}{\tau} \qquad (2.22)$$

Here m_{max} is the maximum value of tree biomass, m_f is the rate of biomass growth of free-to-grow tree of the age t (nutrition area of such tree is considered to be unlimited), τ is the time constant which depends on internal properties of tree and is equal to specific time of tree dying-off (provided the area of growth is absent), $\varkappa$ is the coefficient defining area occupied by tree: $\varkappa = A(m)/A_f(m)$, where A and A_f are the areas occupied by the modeled tree and by the free-to-grow tree respectively. Supposing the area of plot is distributed among plants according to their "demands", we can obtain

$$\varkappa = \lambda^{-1} \; ; \; \lambda = \int A(m) l(m,t) dm \qquad (2.23)$$

where l(m,t) is the tree density within the unit plot.

Analysis of this model (performed, naturally, by numeric methods) made it possible to explain a number of interesting effects. In particular, it was shown by the authors that real even-aged forest stand should be composed of trees provided with different areas of growth. As for trees which are dying-off, their area of growth is bound to be redistributed among the most strong and well provided trees within stand. In that way, the authors account for occurrences of disastrous extinction for some artificial stands.

Subsequent analysis of this model permitted to investigate dynamics of distribution of areas accessible for a tree in the course of growth (Voronov's areas), as well as to describe some specific features of the spatial distribution of trees (Galitsky, Krylov, 1985, Galitsky, Tuzinkevich, 1987).

4. Root competition

When modelling this type of competition, one can discern two approaches.

Within the first approach, to calculate soil resources falling to the share of separate plant as a result of root competition, Korzukhin (1986) applied the same procedure that was used in the task concerning competing for light within the population of horizontal screens. Root systems of plants are supposed to be two-dimensional, and areas of these systems are equal to σ. In case of Poisson distribution of number of plants at the plane, the average quantity of the resource accessible for one plant is equal to

$$I = \frac{I_o}{N} (1 - e^{-\sigma N}) \qquad (2.24)$$

where I_o is the total quantity of the resource mentioned, N is the number of root systems per unit of area.

System (2.20)-(2.24) may be regarded as the model of stand by which the main competing interaction between trees is a soil one.

The second approach (Karev, Treskov, 1988) by modelling of the spatial competition takes into consideration exchangeability of root system. It's supposed that plants create "common root system" and each plant receives portion of mineral nutrition proportional to the relative portion of its biomass. Let's consider this approach more precisely. Let the plant be characterized by mass m. Denoting density of root system of this plant at the distance Z from it through $\mathcal{W}(m,z)$, we can express density of root system of the whole population in the point Z as follows:

$$\mathcal{T}(m,t) = \int_{0}^{\infty} \mathcal{T}(m,Z-y) N(t,m,y) dm\, dy \qquad (2.25)$$

where $N(t,m,z)$ is the density of number of root systems of plant in the point Z. Absorption rate of food resource is given by $V(Z,t) = \min(E_0, A/\mathcal{T}(Z,t))$, where E_0 is the constant of resource concentration in the soil and A is the maximum value of absorption rate. As a result, absorption rate of resource by the whole root system of plant which has a biomass m can be expressed in the point Z as

$$C(t,m,z) = \int_{0}^{\infty} \mathcal{T}(m,z-y)\, V(y,t) dy \qquad (2.26)$$

When calculating densities of root system in the point Z, function $\mathcal{T}(m,z)$ is assumed to be a hyperbolic one:

$$\mathcal{T}(m,z) = \frac{m}{1+\alpha^2 z^2} \qquad (2.27)$$

To obtain this dependence, the following considerations are used. It's supposed that biomass of root system decreases proportional to the cube of distance from plant. Within model describing "vertical section" of cenosis located at the plane, the mentioned decrease should be considered proportional to the square of distance from plant. Hence the formula (2.27) arises.

In the work by Karev and Treskov (1982), the described competition was introduced to model the so-called boundary effect in phytocenosis (sizes of plants at the boundary of their natural habitat differ from respective sizes within this habitat). The law of plant development was selected in the form of equation referring to Bertalanffy's type:

$$\dot{m} = \min(C, E_0 m^{2/3}) - bm \qquad (2.28)$$

where C is expressed by means of formula (2.26), b=const.

It should be noted that description of distributed cenosis proposed by the authors was then generalized in the works by Tuzinkevich (1987, 1988) when describing spatio-temporal dynamics.

There are some works with attempts to model several compe-
ting influences upon growth and development of forest stand.
Models developed by Gurtsev and Korzukhin (1988) belong to such
works.

Equation for growth of individual is based upon the model
(Kull, Kull, 1989) describing growth of mass m for pine and
distribution of assimilates y with the aid of balance system

$$
\begin{cases}
\dot{y} = \Phi(m) - cy - R(m) \\
\dot{m} = cy - V(m)
\end{cases}
\qquad (2.29)
$$

Here $\Phi(m)$ is the net photosynthesis, $R(m)$ is the loss owing
to respiration, $V(m)$ is the mass loss on account of dying-off,
C is the specific rate of transition of assimilates into biomass.

Supposing distributing of assimilates occurs essentially
faster in comparison with change of tree mass $(\dot{y} = 0)$, the equa-
tion for dynamics of tree mass was obtained which, taking into ac-
count allometric relation between tree diameter and tree mass
$D = Km$, expressed by using of discrete time, could be written as

$$
D(t+1) = D(t) + aD^{\alpha} F(D, H, \varphi) - dD^{\delta} \qquad (2.30)
$$

Here function $F(D, Z, \varphi)$ expresses change of size increment depen-
ding on competing for light and for area of growth. This depen-
dence has a hyperbolic form. When deducing the law concerning
competing for light, tree crowns were modelled by means of
isosceles triangles, and the influence of both direct and dif-
fused light flows was considered. Root system was modelled by
means of intersecting rectangles. This model was fitted on the
basis of observation data obtained when pine planting in the
Moscow region. Thus, some of parameter values were taken from
observation data, other values were borrowed from literature and,
finally, certain part of necessary parameter values was selected
with the aid of computer calculations proceeding from condition

that solution of equation (2.20) should be approximate to the growth trajectory obtained on the basis of experimental data. Such approach permitted to verify stability of model solutions relative to variation of some parameters.

2.3. Besides analysis of dependences associated with characteristics of trees within forest stand, models of stand dynamics are applied to analyse strategies of growth and development of plants depending on environmental conditions. One of the principles used by modelling of biological objects (in particular, by modelling ontogeny of plant growing within association) is the principle lying in the fact that organism itself optimizes its functions from the standpoint of natural selection. It's considered this principle allows to account for adaptation properties of biological objects. Plant is able to distribute its resource both for growth (development) and for production of progenies (seeds). The optimization strategy may be reduced to two feasible options, namely maximization of productivity (biomass increment) and maximization of number of progenies (rate of population growth). It is clear that both options may be realized in practice.

The first of mentioned strategies was applied within models developed by Rachko (1979), Oja (1985, 1986) to describe distribution of assimilates among plant organs, as well as within a number of other models, for example, Nilsson's model (1977). The second strategy corresponds to the principle of differential survival of individuals in the form of Holdane-Semevsky (Semevsky, Semenov, 1982). This strategy was applied within models by Vorotyntsev (1985), Insarov (1975) and some other Soviet and foreign authors.

Applying of the first strategy by modelling is described in detail in the preceding section of this article. Now we consider the second strategy being applied within the framework of works by Korzukhin (1985) and by Korzukhin and Ter-Mikhaelyan (1987).

The first model describes changes of tree biomass on condition that among the individuals within forest stand there is competing for resource, namely, for light falling upon individual

simulated by means of "horizontal screen", or for mineral nutrition. This model represents subsequent development of Insarov's model which described growth of the mass of object by means of system

$$m_{i+1} = (1+\alpha_i a)m_i$$

$$J_0 = \sum_{i=0}^{N} (1-\alpha_i)am_i \qquad (i=\overline{0,N-1}) \qquad (2.31)$$

Here a is the quantity of resource, $0 \leq \alpha_i \leq 1$ is its share used for growth, J_0 is the coefficient of reproduction.

Strategy realized within Insarov's model included the following: growth up to a certain age, and then reproduction process. The switching point was determined on the basis of dependence of resource on age.

Within described model by Korzukhin, mass is considered to be proportional to the surface of individual[x], and the quantity of accessible resource is expressed (according to the competition model) as $a_i = a \exp(-\beta Nm_i)$. The given model may be presented by

$$S_{i+1} = (1+\alpha_i a \exp(-\beta NS_i))S_i$$

$$J_0 = C \sum_{i=1}^{N} (1-\alpha_i)S_i a \exp(-\beta NS_i) \qquad (2.32)$$

where C is the number of seeds produced in the presence of the unit resource, β is the value describing the competition intensity. The numbers of population N are considered constant (model parameter).

The strategy of ontogeny is searched (i.e. the dependence of the resource share α_i on the total resource value N, on the initial area S_0 and on the longevity a). This strategy should

---

[x]This suggestion is justified for trees with leaves of "zero thickness" (infinitely thin screens); in case of conifers, it should be accepted $S_i \sim m^{2/3}$.

provide maximum amount of seeds produced by the individual for the whole lifetime: $\alpha_i = \alpha(N, S_o, a)$. Such strategies were found in the mentioned work. In this connection, the space of parameters N, S_o, a is divided into areas by which own optimum strategy may be realized to provide maximum amount of seeds.

This model was not identified. A possibility to realize the obtained strategies was examined indirectly by means of introducing of equation for population numbers into the model, as well as through investigation of properties of the mentioned numbers when applying different strategies. In particular, it turned out well to obtain effect of the observed stabilization of numbers owing to adaptive change of fertility of the individual. As generalization of model (2.31), model developed by Korzukhin and Ter-Mikhaelyan (1987) may be regarded. Within this model, an approach is formulated to describe optimum ontogeny of plant by taking into account both survival and competition. In this general case, model is given by

$$
\begin{cases}
n_{i+1} = V\left(\dfrac{\alpha_i f(a)}{f_{max}(a)}\right) n_i \\[2em]
m_{i+1} = m_i + \beta S(m_i) f(a) - b(m_i) \\[2em]
R = \dfrac{1}{n} \sum_{i=1}^{N} \mathcal{P}(\gamma_i, S(m_i) f(a), m_i) u_i \to max \\[2em]
\alpha_i + \beta_i + \gamma_i = 1
\end{cases}
\tag{2.33}
$$

Here $a = a(m_i, n_i)$ is the resource amount accessible for an individual within population composed of individuals with biomass m_i; $S(m_i)$ is the absorption surface of individual; $f(a)$ and $f_{max}(a)$ are the specific and the maximum specific photosynthesis of individual respectively; $\alpha_i, \beta_i, \gamma_i$ are photosynthesis shares distributed among protection, growth and reproduction of individual respectively; $b(m_i)$ is the loss owing to respiration of individual. Within this model, reproduction is described by means of

function $P(\gamma_i, f, m_i)$ which represents the amount of seeds pro-
duced at the i-th step by the individual with biomass m_i when
the reproduction resource is γ_i.

The first equation of the model describes dynamics of num-
bers depending on survival V which is supposed to be a convex
function. The second equation represents equation of mass balance
written in the difference form.

In the mentioned work, a special case is mentioned when
specific photosynthesis doesn't depend on absorption surface
(effect of self-darkening doesn't take place) and is propor-
tional to the mass of individual modelled by a horizontal screen:
$S(m) \sim m$, $E = f(a) = ae^{-\lambda m_i n_i}$; in this case, survival V is linear
(concerning its argument), and individual is able to protect
itself against environmental influences: $V = u \cdot (1-u) \alpha_i$. Loss
arisen owing to photosynthetic process is proportional to
photosynthesis itself.

And, finally, the given work examines also more special
case concerning growth of individual without any competition;
$\lambda = 0$.

Analysis of these models brought to light a number of
interesting strategies of tree development. Chances of reali-
zing these strategies are also discussed in the given work.
In particular, the following effect is revealed: one of the
reasons leading to growth of tree being ceased (besides the
reason which has been known before and consisted in respiration
and photosynthesis losses being equal) is the switching of
the photosynthetic productivity to the seed production.

It is obvious that selection of the optimizing functional should be realized with taking into account biological properties of the object investigated within the framework of specific task.

It should be noted that models of the type (2.14), (2.20), (2.33) were applied (Karev, 1984, Antonovsky, Korzukhin, 1986, etc.) both for investigation of quality effects intrinsic to behaviour of stand under certain conditions and for working out of forecastings. In particular, in case of two-species association the synecological (competitive) effect of compensation was obtained which consisted in the following: the change of biomass or other structural characteristics would be stronger without competition. The assessment of model parameters (or the assessment of external factors which influence them) permits to discern options of the behavioral strategies when changing of environmental characteristics.

2.5. We describe the approach to modelling of forest stand with the aid of balance relations of the type (1.13) (model developed by Ross) which include functions selected phenomenologically in conjunction with coefficients taken partly from experimental data. As an example of such approach, we may mention the model by Bogatyrev (1988) intended for description of behaviour of three-species plant association near the boundary which separates taiga and tundra. The model variables are the values of biomass of conifers (X_3), of moss (X_1), of herb and shrub layer (X_2), of litter (X_4), as well as of dead organic matter (X_5). This model may be presented as

$$\left\{ \begin{array}{ll} \dot{X}_i = R_{oi} - R_{i4} & i=\overline{1,3} \\[2em] \dot{X}_4 = \displaystyle\sum_{i=1}^{3} R_{i4} - R_{40} - R_{45} - R_4 & (2.34) \\[2em] \dot{X}_5 = R_{45} - R_{50} - R_5 \end{array} \right.$$

Each equation of the model represents detailed equation of Bertalanffy's type by which productivity and folliage fall are described by members proportional to the exponent of one of the variables multiplied by coefficient which expresses dependence on external parameters, such as temperature, water conditions, nutrition conditions, vegetation type. For example:

$$R_i = m_i x_i ; \quad R_{K4} = m_{K4} x_K \quad (i=4,5; \ K=\overline{1,3}; \ m_J = const)$$

$$(2.35)$$

$$R_{o4} = F_i \varphi_i (T_M, X_3) G_i (X_3) f_i (X_5) H_i (W) \mathcal{X}_i (X_3)$$

where F_i is the coefficient intrinsic for vegetation type; $G_i(X_3)$ and $f_i(X_5)$ are the functions simulating dependence of annual increment on the deficiency of PAR under canopy $G_i(X_3) = \exp(-\alpha_i X_3)$ and on the deficiency of mineral substances in soil $f_i(X_5) = \exp(-a_i/X_5)$. The annual increment is given by $\mathcal{X}_i(X_3) = 1$ for $i=1,2$, $\mathcal{X}_3(X_3) = K_x^\gamma$ $(0 \leqslant \gamma \leqslant 1)$. Dependence of biomass increment on water conditions may be expressed by function $H_i(W) = \exp(-b_i(W_i - W^x)^2)$, where precipitation amounts W, b_i, $W^x = const$ and $W^x = W^x(P_M)$.

In accordance with conception of zonal climax developed by Ph.Clements, the main factors influencing stand development are temperature T and precipitation amount P. Within this model, it is supposed that influence of climate parameters upon state of ecosystem is mediated by creation of microclimate under the tree canopy with respective parameters T_M and P_m. And, finally, the main factor influencing forest stand and being investigated within this model is the temperature rate described by likelihood function chosen on the phenomenological basis, namely

$$T_M(X_3,T) = T \cdot \begin{cases} f(X_3), & 1 \leq f(X_3) \neq T_A/T \\ T_A/T, & f(X_3) > T_A/T \\ 1, & f(X_3) < 1 \end{cases} \qquad (2.36)$$

where $f(X_3)$ is the quadratic polynomial which reachs maximum by finite values of X_3. Functions $\varphi_i(T_M)$ which appear in equations (2.34) and (2.35) can be expressed through climate parameters T_A and T_y, where T_A is equal to "temperature of tundra" and T_y corresponds to "temperature of taiga".

It was shown in this work that, depending on values of parameter T (as well as on "steepness degree" of function f), both one state of stable equilibrium coupled with two states of unstable one and two states of stable equilibrium separated by one state of unstable equilibrium may exist within the given model. Areas which correspond to those states are interpreted respectively as areas where hysteresis doesn't take place or, on the contrary, exists while changing of the tundra vegetation by the taiga one. The effect of hysteresis consists in system being in different states (tundra or taiga states) at the same temperature depending on the preceding history. Thus, according to the model (2.34), one can judge by the value of variable X_3 (biomass of conifers) and by the value of temperature whether transition from "taiga" to "tundra" would be realized uninterruptedly and smoothly by temperature increase. (Within hysteresis area, such transition is bound to happen in sharp and uneven way).

The model has been identified on the basis of great number of observation data concerning vegetation and climate of boreal forest. Some of model coefficients have been selected when. identifying[x].

3. Age dynamics

3.1. Detailed description of forest associations includes analysis of their age structure. For some populations, it is impossible to construct any adequate models leaving out of account age structure. Such analysis for populations of various kinds has been carried out from the beginning of this century starting with the works by Lotka (1925), Volterra (translated into Russian in 1931) on the basis of linear models of three types, namely: both temporal and age discrete models, temporal discrete and age continuous models, both temporal and age continuous models. Let us denote $l_a(t)$ the density of number of individuals which have reached age a to the moment t, c_a the intensity of transition from one age group into another group, β_a the density of birth rate of the respective age group, μ_a the mortality rate, φ_a ($\varphi(a)$) the initial age distribution. Within models of the first and the second type, n age groups may be singled out. Density $l(a,t)$ is a vector function: $\{l(1,t),\ldots, l(n,t)\}$.

As an example of the first group of models, the following system may serve:

$$
\begin{cases}
l_1(t+1) = \sum_{1}^{n} B_a l_a(t) \\
l_{a+1}(t+1) = C_a l_a(t) \\
l_a(0) = \varphi_a \\
a = 1,\ldots,n
\end{cases}
\tag{3.1}
$$

[x] In our opinion, mathematical structure of model and number of its parameters allow to describe even more complicated hanges of behavioral conditions, such as periodical conditions. This work requires carrying out of subsequent investigations (see Bazykin, Kuznetsov, Khibnik, 1985).

Models of the second type are described by differential equations

$$\begin{cases} \dfrac{dl(a,t)}{dt} = Ll \\[2mm] l(a,0) = \varphi(a) \\[2mm] a = 1,\ldots,n \end{cases} \qquad (3.2)$$

where transition matrix L may be presented in the most simple case by

$$L = \begin{pmatrix} B_1 & B_2 & \cdots\cdots & B_{n-1} & B_n \\ C_1 & 0 & \cdots\cdots & 0 & 0 \\ 0 & 0 & \cdots\cdots & C_{n-1} & 0 \end{pmatrix}$$

and it is called Leslie matrix. (To describe populations of more complex organization, other forms of matrix L may be used).

Characteristics of solution $l_a(t) = \{l_a(t),\ a=1,\ldots,n\}$ of the models (3.1) - (3.2) are completely determined by the properties of transition matrix. Depending on the distribution of birth rate among age groups, solutions may converge either to the stationary distribution or to the periodical balanced one (in the second case, it is usual to say that population waves oscillate around Leslie distribution). Converging to the balanced distribution proceeds fast in an exponential manner.

These results were obtained in the initial form by Leslie himself (1945) and then generalized and supplemented by many authors who investigated cases of more complicated organization of transition matrix, in particular, influence of mortality within age group (cohort) upon the stable distribution (review of works and original results are given in the monographs by Himmelfarb et al., 1974 and by Poluektov et al., 1980).

According to the works by Lotka and Sharp (Poluektov et al., 1980), models continuous by time and age (models of the third type) are written as

$$\begin{cases} \dfrac{\partial l}{\partial a} + \dfrac{\partial l}{\partial t} = -\mu l \\[4mm] l(a,0) = \varphi(a) \\[4mm] l(0,t) = \displaystyle\int_0^{\infty} \beta_a\, l(a,t)\,da \end{cases} \qquad\qquad (3.3)$$

The last equation of this system defines the law of birth rate within a population. From the mathematical point of view, it represents the integral boundary condition and transforms the system (3.3) into independent mathematical object. The main result concerning the model (3.3) is the theorem of Lotka-Sharp: there exists an "internal rate of population growth", i.e. constant λ determined by mortality rate μ and by birth rate β, such that if $\lambda < 0$ then $l(a,t) \to 0$ by $t \to \infty$; if $\lambda \geq 0$ then normalized density $\exp(-\lambda t)\, l(a,t)$ converges to the "stable" limit distribution $l^x(a,t) = A(a)T(t)$ characterized by the relative value of each age group not being altered in time. The modern formulation of the Lotka-Sharp theorem is given by Webb (1984).

Let us give an example of the model (3.1) being applied to analyse age dynamics of the forest association. In the work by Korzukhin and Ter-Mikhaelyan (1982), such model is used for research of behaviour of population competing for light by which individuals are simulated by means of the "horizontal screens" (see section 2). Survival of the K-th age class $\gamma_K =$ $= 1 - \mu_K$ and seed productivity (fruitfulness) B_K are functions of the average amount of resources received by one individual (to be more precise, they are functions of the specific amount of resources per unit of surface: $r_K = R_K/S_K$, where R_K is the total resource, S_K is the area of surface). In the work mentioned, the case of monotonous competition is considered, namely if γ_K doesn't depend on r_K and fruitfulness is proportional to r_K. Survival of the K-th class is expressed by

$$c_K = a_K e^{-1/2 \quad S_K l_K - \gamma S_{K+1} l_{K+1} - \cdots - S_n l_n}$$

where the first item of the exponent describes intra-age competition, a_K is the density-independent component of survival, γ is the coefficient of light absorption by the individual. Example concerning three-age population of "horizontal screens" is considered in detail in the mentioned work too.

It's obvious variating of competition type leads to constructing of analogous interesting models.

3.2. Influence of resource limiting upon population dynamics being taken into account results in necessity to generalize models (3.1)-(3.3). As an important example, such model may be considered:

$$\begin{cases} l_a(t+1) = C(a,N) l(a,N) \\ l_1(t+1) = \beta(a,N) l(a,N) \\ N(a) = \sum_{a=1}^{K} l(a,N) \qquad a=1,\ldots,n \end{cases} \tag{3.4}$$

where the birth rate β and survival C are dependent on the population density N. Model (3.4) is a generalization of model

(3.1). In a similar way, models (3.2) and (3.3) were generalized too; in this connection, a case was investigated when mortality μ depended on population density. The model (3.4) was first researched by Leslie. Later many works have been devoted to the similar investigations (Poluektov et al., 1980).

In the work by Antonovsky and Korzukhin (1983), model approach was applied to simulate the well-known phenomenon of forest dynamics, namely variations of age structure for population of trees regarded as strong edificators. For the purpose of modelling, the authors applied hypothesis about existence of optimum development for the young growth by certain density of adults. From mathematical point of view, this supposition came to the introducing of non-linearity into the model (3.2). To be more precise, within the most simple two-cohort system

$$
\begin{cases}
\dot{X} = py - \gamma X - fX \\
\\
\dot{Y} = fX - hy - py
\end{cases}
\tag{3.5}
$$

(where X is the density of young growth, y is the density of adults); it is supposed $\gamma(y)=(y-a)^2+b$. It was shown that, depending on relations between parameters p,h,f, the system might be characterized by one, two or three states of equilibrium, i.e. by certain relationships between birth rate and mortality this model allowed the stationary conditions to be realized with nonzero numbers of cohorts. A possibility to reach such conditions depends essentially on the initial concentrations of cohorts. It should be noted that existence of the mentioned conditions is impossible within the framework of linear model.

Korzukhin (1980) examined the three-cohort model of similar structure:

$$
\begin{cases}
\dot{X} = pZ - \gamma(x,y,z)x - fx \\
\dot{Y} = \alpha fx - Py - q(y,z)y \\
\dot{Z} = \beta py - hz
\end{cases}
\tag{3.6}
$$

It was shown that within this model there might be realized not only nonzero stationary numbers, but also stationary periodical conditions if the young growth was mainly suppressed by trees of the third cohort (by $q(y,z)=$const and $\gamma(x,y,z)=\gamma(z)$). Validity of these assumptions was discussed in the work by Gavrikov (1985) where it was shown that stable oscillations were impossible within the framework of given model in the presence of sufficiently realistic suppositions concerning properties of coefficients of the system (3.6). Existence of periodical conditions proved to be feasible within the generalization of model (3.6) proposed by Korzukhin, Matskiavichus, Antonovsky (1989):

$$
\begin{cases}
\dot{X} = V(\gamma\delta)(f+pz) - x \\
\dot{Y} = x-y \\
\dot{Z} = y-z
\end{cases}
\qquad (3.7)
$$

Within this model, influence of seed influx from the adjacent areas is taken into consideration. This influx is simulated by means of nonlinear function $fV(u)$ with argument u dependent on the total leaf area of trees belonging to all three cohorts: $u= \gamma(S_1x+S_2y+S_3z)$. System (3.7) was investigated for different functions V and for different values of parameters f and γ .

In the same work, authors gave much attention to discovering of the periodical conditions within discrete models of the type (3.4). Model (3.4) was generalized by means of the consecutive introducing of density-dependent component of survival and density-independent component of mortality into each equation bearing a relation to cohort numbers. Functions of growth and survival were variated within the models. Parameter space (composed of values which describe growth, survival and mortality) was divided into three areas corresponding to specific types of the dynamical behaviour. The prerequisites necessary for existence of periodical conditions were found. It was also shown a possibility to describe age waves observed in reality.

Models of the type (3.1)-(3.3) served as a basis for model-
ling of influence of insects upon numbers of population with
age structure (Antonovsky et al., 1987, Samarskaya, 1989,
Boulange, 1989). Within the framework of these approaches, in-
teresting mathematical results were obtained which could be
brought into correlation with the real dynamics of population
numbers.

3.3. According to modern conceptions, dynamics of popula-
tions is described in the most detailed and adequate way within
the framework of theory of structured population models. Within
such models, every individual is described by its age a, as well
as by a certain set of dynamical variables reflecting the inner
structure (such as biomass, sizes, etc.). General population
processes are growth, reproduction and death. Their intensity
depends on age of individual and on its state, as well as,
probably, on general population characteristics (for example,
on the total population size). Equation related with dynamics
of numbers within age groups is also included into models mentio-
ned.

An example of structure model of forest stand when time and
age are supposed to be discrete was given by Korzukhin (1989).
In this work the scheme for seasonal reproduction of two-age
population was constructed, namely

$$\begin{cases} m(a+1, \ t+1) = m(a,t)+S(m)A(\varphi[m,n])-R(m) \\ m(1, \ t+1) = f \\ n(a+1, \ t+1) = w(a)V([m,n])n(a,t) \end{cases} \qquad (3.8)$$

where n(a,t) is the number of trees per hectare, m(a,t) is the
mass of trees of age a at the moment t, A is the specific assi-
milation at the moment t, f is the influx of seeds, w(a) and
V([m,n]) are respectively density-independent and density-depen-
dent components of survival (arguments of functions V and φ
describe competing for light or for nutrition given by the model

of screens: $[m,n] = \exp(-\gamma \sum S_L n(a,t))$, where S_L is the area of tree surface). Within the framework of this model, the author applied numerical methods to find periodical solution $n(a,t+0) = n(a,t)$ observed in one- or two-species stands just where the given model was being identified.

In the work by Korzukhin, Matskiavichus and Antonovsky (1989) the model (3.8) was generalized in three directions:

1/. specification of dependence of young growth mass on fruit-fulness of the rest of cohorts $\beta(R,A)$ and on the total survival u:

$$n(1,t+1) = u(f + \sum \beta(R,a)n(a,t)) \qquad a=1,\ldots,n$$

2/. specification of competition model with taking into account shading of the part of crown:

$$R(a,t) = I_0 \sin \varphi \exp(-\tfrac{1}{2}\gamma S(a,t)n(a,t) - \gamma \sum_{\mu=i+1}^{n} S(\mu,t)u(\mu,t)$$

(coefficient $I_0 \sin \varphi$ gives the value of illumination under the crown canopy);

3/. specification of properties of density-dependent component of survival

$$V(a,t) = 1 - K(1 - A(R)/A^{max})^{\sigma}$$

The obtained model described behaviour of age-distributed popula-tion which served as a basis for verification of this model with utilization of great number of data (see, for example, Katayeva, Korzukhin, 1987). In this connection, some of coeffi-cients were taken from literature and another part of them was variated by means of computer calculations. Within space of model coefficients, on the basis of numeric methods the areas were found which correspond both to stable distribution and to stable oscillatory conditions (in a number of cases, with two or three frequencies). Within this model, two invariants came into being, namely amount of light absorbed by the unit surface of phytocenosis and oscillation period. It should be noted that sufficient steepness of function V was necessary for arising of oscillations mentioned.

At present, structure models are widely used (including models of age structure) when age and time are supposed to be continuous (see special issue 'Computer & Math', 1983, Oster, 1977, Poluektov et al., 1980). In its sufficiently general form, dynamical model of structure population is given by the following system

$$\dot{x} = F(x,a,P_1); \qquad a=1$$

$$\frac{\partial l}{\partial t} + \frac{\partial l}{\partial a} + div(lF) = -\mu l \qquad (\mu = \mu(x,a,t,P_2))$$

$$l(x,o,t) = \iint \beta(x,a,y,P_i)l(y,a,t) \, da \, dy \qquad (3.9)$$

$$l(x,a,o) = \varphi(x,a)$$

$$P_i(t) = \iint g_i(y,a)l(y,a,t) \, dy \, dt$$

Here the first, second and third equations of system determine dynamics of structure variables and numbers of population. The third equation gives the rate of arising of newborns, whereas the fourth equation determines the initial age distribution. Functions P_i have different sense for concrete applications. For example, they are used, within stand models, to calculate amount of external resource (light, moisture) received by a tree as a result of competition.

As for the general model (3.9), comparatively few results are known. The unique existence theorem (which is the direct generalization of Gurtin-MacKamey theorem) was proved (Tucker, Zimmerman, 1988), as well as the questions concerning existence and stability of stationary solutions were investigated. Methods for analysis of nonlinear models of special type (so-called "separable models) were obtained (Boulangé, 1988, Karev, 1989).

As regards linear structural models, their asymptotic behaviour is known at present. The first results concerning special case of the model with one structural variable were obtained by Webb (1985), and the general case was analysed in the works

by Karev (1987, 1990) who succeeded In generalizing Of Lotka-
-Sharp's theorem and presented manifest form of stable distribu-
tion through the initially given values.

Not going into details of the general theory of structural
population models, we give an important example of its applica-
tion when modelling forest stand dynamics (Berezovskaya, Karev,
1990) on the basis of conception about layer-mosaic characte-
ristic of spatial-temporal structure of stands (This conception
is developed in works of Uranov's school (Smirnov et al., 1990,
Buzykin, Sekretenko, Chlebopros, 1989), as well as, in the
most simple form, in the numerous simulation "gap-models").
When considering the mentioned conception with some simplifica-
tions, a tree population can be presented at any moment as the
aggregate of loci (sections) described by different age, density
of tree number, size and (in case of association) species compo-
sition. The loci undergo changes and develop asynchronously in
time. Having formalized the described suppositions, asymptotic
(climax) behaviour of model was examined when considering forest
stand as a population of cenons, or one-species loci, which are
characterized by the following features: a cenon occupies fixed
area; at any moment, cenon can be described by set of structural
variables, as well as by density of tree number and by age dis-
tribution; the birth of a new cenon occurs after the death of an
old one at the same place and with the same probability depen-
ding only on the state of an old cenon; dynamics of an individual
tree being a part of cenon depends essentially on the interaction
with neighbouring trees within given cenon and doesn't depend on
the state of trees in other cenons. It is proved that by very
sweeping assumptions concerning concrete description of dynamics
for a separate cenon, the distribution of population converges,
on the whole, fast to a stable distribution. Form of this distri-
bution can be found for general case and expressed through the
initial values and rates of change of the model dynamic variables.
As models for describing of separate cenon, any models of even-
-aged forest stands may be used (including models examined in
section 2 of the given review). Thus, qualitative inferences

from the above-mentioned ecological works concerning existence of the stable distribution within the framework of layer-mosaic conception of structure and dynamics of forest stands assume a character of precise mathematical statement for the examined class of models.

4. Simulation models

4.1. At present, models describing dynamics of forest association as the aggregate of successions within its natural habitat are widely practised. The ecological considerations being the basis of these models are similar to layer-mosaic conception described in section 3. To be more precise, at different sites in the forest, in consequence of dying off, fires, etc., it takes place the permanent process of arising of gaps in a fortuitous way. Within these gaps, it takes place forming of successions which are defined as changes of vegetation types occurring at the appointed time (such changes depend on characteristics of the locality). Spatio-temporal dynamics is given by the mosaic accumulation of population loci of tree and herb plants changing each other.

Among these models, we mention the broad class of so-called gap-models used to simulate behaviour of forest association by means of computer calculations. The first of gap-models is the model developed by Leak (Leak, 1970) which simulates succession with the aid of simultaneous probabilistic taking into account of two processes, namely reproduction and extinction (Oja, 1985). At present, a great number of such models have been proposed, for example, JABOWA (Botkin et al., 1972 a,b), TEEM (Shugart et al., 1974), SDF (Sollins et al., 1976), etc. The main task to be solved with the aid of them consists in the state of homogeneous forest tract to be cleared up in a given number of steps. With that end in view, several sites of the fixed area (gaps) are chosen within forest tract. There are some trees at each site, but initially these sites may be empty. At every moment, each tree is described by a certain set of typical parameters, namely: species, height, total leaf area. For each tree the growth equation is also given which depends on external environmental para-

meters, as well as on the chosen type of tree model. Reproduction and mortality of trees within a site are given by means of some kind of random process. Within models JABOWA, FORET, FORSKA (1989), the main block is growth equation containing a member that takes into account stand density. Within model JABOWA (which marked, virtually, the beginning of this type of models), the growth equation is similar to equation (1.6) supplemented with coefficients which convey dependence on the local temperature conditions, as well as influence of light conditions according to the law of Monsi-Saeki (crown of modelled tree is presented as a horizontal or vertical screen, and subsequently as a cylinder).

In that way age structure (even-aged stands are considered more often) and stand valuation characteristics are calculated for the moment t. The behaviour of forest is obtained by means of calculation and finding average dynamics of many gaps. The advantages of these models consist rather not in the way of their constructing but in the large-scale direction of attention (fulfilled by the adherents of this approach) towards forests growing under diverse ecological conditions (Korzukhin, 1989). So, model FORET (Shugart, West, 1977) was used to study changes in the normal process of succession under the influence of fungus disease which caused death of one of American chestnut species. Model KIAMBRAM (Shugart et al., 1980 a,b) simulates successions in subtropical forests of Australia, whereas model FORSKA is intended for describing successions in the boreal forests of West Europe. Gap-models are used to study influence of fires upon forest successions (Shugart, Noble, 1981).

We may note that gap-models are very visual in biological respect and don't require complicated theory and mathematical means for applying them. Coincidence with reality has usually semi-quantitative character. Owing to being too bulky, these models don't permit any analytical investigation and, therefore, are good only for simulation purposes. Furthermore, from the moment of their arising these models have kept practically unchanged the block for describing of tree growth (it doesn't

correspond any more to modern standards), as well as description of reproduction which doesn't take into consideration age distribution of reproductive individuals within a population. In our opinion, it would be highly promising to combine computational algorithms developed by gap-modelling, as well as methods of adapting for diverse tree associations to be modelled, with thorough theoretical propositions of the layer-mosaic conception.

To determine the state of forest association and to forecast directions of its development, it may be useful to compare the observed distribution of population characteristics with the climax distribution concluded on the basis of model.

These developments also provide a focus for the development of the BOFORS model, a computer simulation model capable of reproducing the structural and floristic dynamics of boreal forests throughout its range in Eurasia and North America (Shugart et al. 1991). The BOFORS model is one of a set of models designed to emphasize the growth, birth, and death of individual trees on small elements of the landscape (ca 1 ha). The minimum time resolution of this model is 1 year (the model computational step) and the maximal time resolution is limited by the degree to which phenomena not included in the model become important at longer and longer time scales. Earlier models of the same genre' have been used to simulate prehistoric changes in vegetation in response to climatic change over the past 20,000 years.At a minimum, the spatial resolution of the BOFORS model is the computational element scale (>1 ha). Most of the applications of this class of models have been at the scale that is represented by 50 to 100

computational elements -- on the order of a few hundred ha or less. Using modern computers it is possible to run the model for selected sample locations throughout the boreal zone to predict current forest conditions over successional time and to produce expected responses of forests to environmental changes.

The BOFORS model was a shared development of forest ecologists from several nations (including the USA and USSR), and is the first global scale model of the dynamical change of a biome. There are "community models" developed by scientists in the atmospheric sciences and there is a long tradition of coordinated collection and sharing of data by several of the subdisciplines in the geophysical sciences. In general ecological scientists have been less able to develop such closely coordinated modeling and experimental projects.

There were several reasons why the boreal forest zone of the northern hemisphere was a logical ecosystem upon which to focus an initial attempt. These uniting features associated with the boreal forests arise both from the nature of the ecological systems themselves, the interests of ecologists working in this region and the proximity of the forests to industrial nations. The boreal forests in some senses are floristically rather simple forests (compared to many tropical rain forests, for example). In most boreal forest stands, one or two species dominate. Most of the dominant trees over a region in the boreal zone can be described in a list of fewer than ten tree species. In comparisons across disjunct continents, one finds the same limited number of genera (*Picea, Abies, Betula, Populus, Larix,*

Pinus) to be repeated elements. The temporal pattern of replace-
ment following a disturbance among the species that represent
these genera is similar. Even though the species names (but not
the genus names) may change among boreal scenes in Europe, Asia,
and North America, the ecological "look" of the landscape reads
similarly. Further, the boreal forests of the world are well
studied forests. They are the holdings of developed nations and
are a repository of valuable timber reserves already well
incorporated into national and international economies. It is
likely that we know more about these forests than any others at
the global level.

The relationship between form and function, or pattern and
process, is a classic ecological theme (Lindeman 1942, Watt 1947,
Whittaker and Levin 1977). Often the pattern-process interaction
is discussed in terms of processes causing pattern in such famil-
iar examples as understanding how ecological energetics and the
thermodynamic constraints shape food-webs (Elton 1927, Lindeman
1942, Odum 1968), or interpreting the processes that cause a
landscape vegetation pattern to have a given appearance (Watt
1947, Whittaker and Levin 1977). It is also clear that patterns
can influence ecological processes to a great degree. For exam-
ple, Bormann and Likens (1979) pointed out the effects of changes
in forest pattern on processes effecting productivity and nutri-
ent cycling. Many ecologists recognize that pattern and process
are mutually causal, with changes in ecosystem processes causing
change in pattern, and modifications in ecosystem pattern chang-
ing processes. In considering the patterns in the boreal
forests, one finds a richness of response that belies the seeming

constancy of processes, and taxonomic similarities across the boreal forests. While the landscape patterns in the boreal forests of the world may be similar in their gross appearance, the generation of these similar patterns may be the consequences of complex, nonlinear reactions among processes and patterns.

4.2. The relationship between dynamics of successions and areas occupied by certain stages of successional development is retraced in the work by Korzukhin and Sedykh (1983) which originates from the work by Shugart et al. (Shugart, Crow, Hett, 1973).

Let us denote P_{jn} the part of territory occupied by phytocenosis being at the stage n (n=1,...,Q) and R the total number of such parts (j=1,...,R). Then dynamics of mentioned parts of area may be described by means of the linear Markovian system

$$P_{jn}(t+1) = P_{jn}(t) + \sum_{s}^{Q} a_{jns}(f)P_{js}(t) \qquad (4.1)$$

where $a_{jns}(f)$ are the probabilities of transition from the successional stage n to the stage s; these values describe both endogenesis and change of stages because of the exogenous disturbances; f are the parameters of climate and physico-chemical state of the atmosphere, t is time. In works by Korzukhin and Sedykh (see, for example, 1983), this model was improved and used to describe spatial-temporal dynamics of facies, i.e. parts of territory occupied by identical elements of plant cover being at the same successional stage. In that case, modification of the model (4.1) with taking into account such influences as fire or invasion of phytophagans may be expressed by

$$r_i(t+1) = r_i(t) + \sum P_{Kij}r_K(t) - r_i(t)\sum P_{iKj} \qquad (4.2)$$

$$(i=1,...,n)$$

where $r_i(t)$ is the part of territory occupied by facies being at the given stage i of successional system within the framework of considered territory, P_{iKj} is the probability for facies to transit from the state i to the state K per time unit under the influence of the indicated factor J , $P_{iKj}=P_{iKj}(f)$. (Value $J=1$ corresponds to the natural course of events, namely to the endogenic successional lines, so that $P_{i,i+1,1}=1/\tau_i$, where τ_i is the duration of stage i). The same model served as a basis when analysing spatio-temporal dynamics under the influence of fires (see Ter-Mikhaelyan and Furiayev, 1988)[x]. The description of dynamics is realized here on the landscape basis: within the considered territory, the so-called wildernesses are marked out, and the whole territory may be presented as "mosaic" of wildernesses while each of them corresponds to own successional series and to own number of successional stage. Wildernesses are considered to be closely connected with each other. Only those fires are taken into consideration which "throw back" the process of forest forming to the zero state (burnt out place in the forest), whereas influence of faint fires should be ignored. As essential factors of fire spreading, one should consider the degree of fire ripeness of stands within the given wilderness and within adjacent ones, as well as the frequency of fire arising within the given wilderness. These values (presented as probabilities of transferring of fire from one place to another and probability of fire arising respectively) depend only on the type of wilderness and don't depend on its location within modelled territory. Within model itself, wildernesses are simulated by means of vertices of square lattice of size lxm. At the moment t, vertex (i,j) is in the state τ ; with probability q, a fire may arise at this vertex or be transferred from the adjacent vertex $(i\pm1,J)$, $(i,J\pm1)$; the given vertex may be burnt down with probability P_τ transferring, at the same time, into the state 0 ("burnt out place") and turning into the source of fire for other vertices. In case the fire doesn't arise up to the moment t+1, age of vertex should be in-

---

[x]This work includes also review of modelling such type of influences.

creased by 1. Thus, in the course of dynamics the spatial inter-
action is realized by means of taking into account probabilities
of fire arising within each wilderness, fire transfer from one
wilderness to the adjacent one and transfer of seeds (being at
the stages of reproductive age) to the burnt area. This model
was verified on the basis of data referring to the fire dynamics
of forests in Minnesota, USA. It showed good coincidence and
simulated a number of interesting effects of this dynamics.

4.3. Combination of models referring to the types (3.8) and
(4.1) was applied by Korzukhin et al. (Antonovsky, Korzukhin,
1986, Korzukhin et al., 1985, etc.) for the purpose of forecas-
ting when considering joint behaviour of the separate phytoceno-
sis (where competing for light, mineral resource, etc. takes
place) and the family of phytocenoses (i.e. forest association
containing the phytocenosis to be modelled). The simulated ob-
jects are situated in a certain region and differ in spatial and
temporal scales, as well as in characteristic times of vital
activity. It was consedered influence of local factors (such as
microclimate, windfall) and global ones (fires, swamping, etc.)
upon the state of mentioned objects. To forecast faint influences
upon the course of succession, it was assumed that factor affec-
ting the association (it was, basically, temperature) changed the
structural characteristics and their numbers (for example, height
of tree of the i-th species according to the formula $h_i = h_{io} e^{\lambda_i t}$,
where h_{io} is the height of "undisturbed" tree, λ is the index of
change rate which depends on environmental properties). On the
basis of model of the type (3.8), it is possible to retrace dy-
namics of change of mass and species numbers. It turned out well
to obtain synecological (competing) effect of compensation, namely
without competition, change of biomass would be more significant.
Furthermore, on the basis of area model of the type (4.1), aut-
hors calculated influence of disturbing factor upon the average
phytomass of cenoses at the whole territory, as well as upon ratic
of parts of territory occupied by phytocenoses at certain stages
of succession. The compensation effect was discovered, namely:
biomass increment at the level of phytocenosis may be compensated
by biomass decrease at the regional level. Methods developed by

the authors of these models make it possible to discern "mild"
and "hard" factors for the different types of associations, as
well as to apply methods developed in the qualitative theory
of dynamical systems when investigating models. We can note one
more feature characteristic for the given range of works, namely:
identification of models was carried out on the basis of great
amount of data obtained from observations with the subsequent
analysis and classification (see, for example, Katayeva, Korzu-
khin, 1987); some coefficients were selected numerically with the
aid of computer calculations; at the same time, the sensitivity
of model to variating of coefficients was tested, i.e. the ques-
tions of stability were investigated over again. We should empha-
size significance of problem associated with selection of coeffi-
cients and model parameters. Here we can retrace the direct connec-
tion with sensitivity of observations which may be secured under
conditions of the most natural time dispersion of the observed
variables (Sokolov, Puzachenko, 1986). Development and analysis
of method applied for the purposes of identification represent an
independent and complicated task.

4.4. The model developed by Bogatyrev, Kirilenko, Tarko
(1988) may serve as an example of simulation model which directs
toward description of one-species forest stand growing at the
northern boundary of taiga zone and takes into account the age
structure of trees. This model is worked out on the basis of
analytical model (2.34) and represents balance relation of Ber-
talanffy's type for each tree within population (we omit index
here):

$$\dot{X} = \phi(x,\tau) f(T_M, I_M, Z_M) - R(x,\tau) r(V_m, u) \qquad (4.3)$$

Here X is the biomass (kilograms of dry matter), τ is the age
of tree ($1 \leq \tau \leq M^x = 250$ years). The development of stand is
determined by the following factors: average temperature of air
in July $T(C^o)$, average annual velocity of wind $V(m/sec)$, number
of thaws during a year u, PAR intensity I (percentage), amount
of mineral resource Z available and created by population. Simi-
lar to the model (2.34), it is supposed that influence of climate

upon development of trees is realized not directly, namely through creation of microclimate characterized by parameters T_M, I_M, V_M. Productivity $\phi(x,\tau)$ and foliage fall $R(x,\tau)$ are described by functions

$$\phi(x,\tau)=F(\tau)x^{1-x/x_s}, \quad R(x,\tau)=K(\tau)x \quad (x_s=const)$$

"Age functions" $F(\tau)$ and $K(\tau)$ are piece linear functions constructed on the basis of experimental data taken from the literature. "Coefficient functions" (f and r) of the model are presented, similar to relations (2.35), as products of few factors[x]:

$$f(T_M, I_M, Z_M)= \varphi(T_M)Q(I_M)L(Z_M)$$

$$r(V_m, u) = S(V_m)G(u)$$

Dependences of functions Q,L and φ on their arguments are supposed to be hyperbolic ones (of the type (1.15 a,b)), i.e. they reflect existence of limit value for large values of the respective arguments. On the part of arguments, they are expressed through model parameters and linear combination of masses Z for trees located within the vicinity Δ of the considered tree, namely:

$$Z_M = \sum_K \frac{f_K}{d_{jK}^2} X_K$$

where X_K is the mass of K-th tree located within the Δ-vicinity of tree J; d_{JK} is the distance between J-th and K-th trees, $f_K=const$.

<u>Note</u>. Here the hypothesis is used which consists in the following: competing for soil resource within the site is reduced proportional to the square of distance between plants (cp.(2.27)).

---

[x]It would be more natural (especially in case of numerical models) to express dependence of "coefficient" on respective arguments in accordance with Liebig's principle by selecting, at any moment of calculations, the main factor which determines kinetics similar to equation (1.9).

The relationship between illumination I_m under the canopy, radiation I and mass Z_i of trees which form canopy is described by the formula similar to equation of Monsi-Saeki (1.16); ·temperature T_M is expressed through T and Z_T according to formula of the type (2.36) (advantages of this formula are corroborated by the model (2.34)); and, finally, velocity of wind under the canopy V_m is expressed through the velocity of wind V and mass of trees which reduce its influence according to formula $V_m = V(1-qZ_v)$ (q=const). The influence of wind velocity and number of thaws upon the foliage fall is determined respectively by function $S(V_m)$ and $G(u)$ which have an order equal to one minus some power of argument; influence of mentioned variables upon behaviour of model is essentially less than influence of temperature.

Finally, death of tree within this model occurs when tree reachs age limit $i=M$, or by unfavourable combinations of climatic factors, or in case of drying ($\dot{x} \le 0$).

The considered model was identified on the basis of data corresponding to spruce stand and describing climate in the region of northern taiga and southern tundra. Behaviour of forest stand obtained on the basis of model resembled in many aspects the behaviour observed in nature, as well as the behaviour obtained within analytical model (2.34), namely: it turned out well to find areas of parameter values $\mathcal{T}$ where there were 1/. phenomenon of hysteresis, i.e. different phase behaviour at the same temperature depending on the previous history; 2/ development of tree vegetation as a result of climatic fluctuations, formation of "islets" of vegetation of the same type within sites covered with vegetation of another type (for example, afforestation of tundra); this phenomenon accounts for drift of boundary between zones which is observed in nature.

Thus, the model allows to carry out a number of investigations of stand development by different scenarios of climate.

4.5. In conclusion of this section,we mention the hypothesis developed by A.M.Molchanov (1975) about correlation of such ecological concepts as successional series and climax-association.

The author turned his attention to relationship between areas of biomes (which constitute a successional series) and times of development for this series. Hypothesis (called ergodic by the author) may be expressed by means of the following chain of equalities:

$$\frac{S_1}{T_1} = \frac{S_2}{T_2} = \ldots = \frac{S_n}{T_n} \qquad (4.4)$$

In other words, areas $S_1, \ldots, S_n$ occupied by biomes within a climax-association are proportional to own times $T_1, \ldots, T_n$ needed for development of biomes within successional series.

The author proposed a practical application of this hypothesis consisting in evaluation of stands according to data from aerial photographs. One of the theoretical conclusions consists in recognition of meaning of fast stages within succession.

It should be noted that it would be interesting to verify this hypothesis within the framework of above-mentioned spatial--temporal models.

5. Modeling of spatio-temporal dynamics

All above-mentioned processes are local, i.e. all characteristics of ecosystem are taken as average ones for the whole space or, in other words, ecosystem is considered to be spatially homogeneous. To analyse the system of biomes being a part of the total forest association (i.e. to model spatially heterogeneous populations), other approaches are traditionally applied, namely: diffusive approach, integro-differential description, probabilistic approach, approach associated with Markovian processes. We dwell briefly on each approach.

5.1. Diffusive approach dating from A.N.Kolmogorov's works assumes that vital activity of association at any point of habitat space depends only on the state of system at this point, and individuals (or products of their vital activity) move over the space in a stochastic way. Such models are called models of the type "reaction-diffusion". They can be presented as

$$\frac{\partial}{\partial t}(u(t,\bar{x})) = F(t,\bar{x},u(t,\bar{x})) + D\frac{\partial^2}{\partial x^2}(u(t,\bar{x})) \qquad (5.1)$$

where $u(t,\bar{x})$ is the spatial density (at the moment t) of some characteristic of ecosystem, D is the diffusion coefficient.

Within the framework of diffusive approach, it turned out well to describe many phenomena in spatially heterogeneous systems, for example, arising of solutions belonging to the type of "travelling waves" (corresponding to numbers, density and so on) in time, as well as arising of spatial heterogeneities ("dissipative structures") which may be regarded as analogous to mosaic structures of biogeocenoses (Svirezhev et al., 1978, 1972, etc, Razzhevaikin, 1981).

In a number of cases, equation (5.1) may be sufficiently well approximated by the so-called chamber models. By means of the method developed by Bubnov and Galerkin, it is possible to go over from equation (5.1) to the system

$$\frac{du_{iK}}{dt} = f_{iK}(u_{iK},\ldots,u_{nK}) + M_{iK}(u_{in},\ldots u_{ip}) \qquad (5.2)$$

where u_{iK} is the biomass (numbers) of the i-th species at the K-th site, f_{iK} is the intrapopulation interaction of the i-th species at the K-th site, M_{iK} is the influx of migrants of the i-th species to the K-th site, n is the number of species, p is the number of sites.

Dynamical conditions within the framework of system (5.2) (which correspond to the stable oscillations obtained from equation (5.1)) may be in line with both synchronous oscillations all over the space and stationary heterogeneous distribution of numbers U_{iK} (so-called dissipative structures). Correlation between solutions of equation (5.1) and system (5.2), while using example of the model association "two victims, one predator", was retraced by Bazykin et al. (1985). Analysis of the properly worked out system (5.2) made it possible to find non--trivial dynamical conditions and to forecast parameter values

and dynamical behaviour within respective distributed system.

We may note that requirement of randomness (or complete intermixing) assumed as a basis of equation (5.1) and sufficiently justified within the tasks of chemical kinetics proves often to be too strict in case of biological objects. It has been observed that even microorganisms turned out to be able to control purposefully their location in the space within the framework of systems of flowing cultivation (Gorban, Sadovsky, 1988). Nevertheless, solutions of the equation (5.1) prove to be sufficiently useful for a number of tasks.

Logofet (1978) showed the introducing of migration (functions M) into the isotropic medium couldn't stabilize ecosystem described by the model (5.2). Introducing of the anisotropic medium may be simulated by means of adding of "random disturbance" to the right parts of system (5.2) and through transition to equation of Kolmogorov-Foker-Planck by using probabilities of population being located in the certain areas of space. This approach for the models of the type "predator-victim" was developed in the works by Sidorin (1988), Sukhanov (1988). As to associations within the uneven-aged forest stand, analogous models are not known for us.

5.2. We give an example referring to description of association structure within changeable external environment with the aid of model which includes random disturbances. Such model for species structure of plant association was proposed by Sukhanov (1988). As a basis system, Volterra's model was applied. Its application, according to opinion of Mac-Arthur (1970), is motivated by "richness" of plant association, basically, in competing interdependences between species (all plants are regarded as the potential rivals competing for resources of vital importance: light, moisture, mineral nutrition, etc.).

$$\frac{dN_i}{dt} = N_i (\varepsilon_i - \sum_{j=1}^{S} \gamma_{ij} N_j) + V\overline{N}_i \quad n_i(t) \equiv Q_i(N_i) + \mathcal{F}(t) \qquad (5.3)$$

Here N_i is the population density of the i-th species (numbers, biomass or another index expressing abundance of population per unit of environment), t is the time, ε_i is the Malthus' parameter for the i-th species (specific growth rate at the initial stage of populating of biotope on condition that no other species are available). γ_{ij} are the coefficients of influence exerted by the i-th species upon the J-th one, S is the total number of species within association. Within Sukhanov's model, the case when $\gamma_{ij} = \gamma_{ji}$ is considered, i.e. the interaction matrix is supposed to be symmetrical. (This most vulnerable assumption is substantiated by the author on the basis of approximate coincidence of phytomasses, leaf areas and other characteristics of the association which are to be taken into consideration when constructing the given model).

Stochastic environmental influence is modeled by means of Gauss' white noise n(t) characterized by the zero average and the intensity D. Amplitude of this noise depends on numbers of the i-th species (by exceeding VN_i times the achieved numbers N_i). This noise "stirs up" the population permanently and doesn't allow it to be stabilized in the stationary state. As a result, point representing the state of population spreads into some stochastic distribution P(N) which satisfies the equation of Kolmogorov-Foker-Planck

$$\frac{\partial P}{\partial t} = -\sum \frac{\partial}{\partial N_i}(Q_i P) + \frac{D}{2}\sum N_i \frac{\partial^2 P}{\partial N_i \partial N_j} \qquad (5.4)$$

worked out by assuming that noise n_i has the meaning given by Stratonovich. With the aid of method developed by Svirezhev and Logofet (1978), when analysing an equation of the type (5.3) it was found general stationary solution of the equation (5.4) which described stochastic species structure of the competitive association, namely

$$P(N) = \frac{C}{D\prod VN_i} \exp(-\frac{1}{2}\sum_{i}^{S} N_i(2\varepsilon_i - \sum_{ij}N_j) \qquad (5.5)$$

where C is the normalizing constant which can be found from the condition $\int_{-\infty}^{\infty} P(N) = 1.$

In the mentioned work , function P(N) is subjected to analysis for S=1 and S=2. In the first case (S=1), function P(N) may be regarded as bimodal one when assuming existence of some relations between coefficients of intraspecific competition and coefficients of intensity of the influencing external forces. Being bimodal means possibility of the stable existence of populations characterized both by small and large numbers. There is an analogous result for two competing populations which is very interesting. In that case, analysis of function P(N) allows to choose such areas within parameter space which may be in line with species competing with each other strongly or faintly respectively, as well as to account for arising of "spotty" distribution of species within natural habitat.

For cases S=1 and S=2, author of the mentioned work realized Identification of model which is based upon the ergodic hypothesis about existence of populations.

The case of high dimension of competing populations was also considered.

5.3. One more attempt of applying equation (5.1) and its modifications to analyse forest ecosystems was made in the work by Janseitov and Kuzmichev (1981).

To describe mosaic structure of forest stand, its active part was considered as distributed system with the diffusive type of relations. Here the diffusion was applied to model dispersion and germination of seeds, penetration of root shoots, transfer of nutrients and the similar processes. This model is analogous to equation (5.1) by which $u(t,x)$ is the density of physiologically active part of biomass at the point $x(x_1,x_2)$ and function F coincides with the right part of concentrated differential equation of the lagging type

$$\frac{du}{dt} = au(t-\tau) - bu^2(t-\tau) - \lambda u(t) \qquad (5.6)$$

Here a, b, λ are the coefficients describing respectively growth rate without any limiting, degree of competition and intensity of biomass death; τ is the value of lagging.

Within this model there exist oscillating solutions which are brought by the authors into correlation with mosaic distribution of increments and with the mode of changing annual rings of trees in case of the real high-density and homogeneous forest stands.

It should be noted the above-mentioned work may be rather regarded as study of task formulations and drawing of analogies. Thorough investigations and identification of equations (5.1) and (5.6) were not carried out.

The semi-empirical approach to modeling of succession spreading in the space is contained in the work by Moskalenko and Cherkashin (1981) which generalizes a similar approach to studying of successions given in the work by Cherkashin (1981). The models represent systems of differential equations (in the spatial case, such equations include also partial derivatives) intended for describing dynamics of numbers for uneven-aged trees of different species within forest stand. With that end in view, coefficients of dying off are given by empirical functions which depend on age, species, closing of leaf canopy and other characteristics of the simulated trees. Owing to that, the authors achieved good conformity of results obtained from models to available data about the real object to be modeled. However, this approach doesn't account for mechanisms of dynamics, and that leads to difficulties while adapting models to another object and makes more narrow the sphere where models may be applied.

5.4. To our opinion, one of the most general approaches when modelling spatial dynamics of stands is the integral approach. Within the framework of this method, interactions between different parts of spatially distributed systems can be described in a natural way. While modelling, the following assumption is made: the plants located in the different points of space may interact with intensity proportional both to distance between individuals and to their sizes. In other words, dynamics of individuals depends not only on their state but also on parameters of biogeocenosis within some vicinity of individuals. This approach

is presented in the above-mentioned work by Karev and Treskov (1982) concerning analysis of boundary effects in biomes which interact by taking into account root competition. General development of this approach was carried out by Tuzinkevich (1987, 1988). On the basis of Bertalanffy's equation (which simulates the rate of changing of density of plant biomass), he proposed the model of plant growth within n-species association:

$$u_i(t,x) = \int_M \alpha_i(x,y) u_i(t,y) dy - Q_i(u_i(t,x)) \cdot$$
$$\cdot \int_M \beta_{ij}(x,y) u_i(t,y) u_j(t,y) dy \qquad (i=\overline{1,n})$$

(5.7)

where $\alpha_i(x,y)$ is the part of biomass u_i spreading from the point y to the point x of space M, β_{ij} is the part of biomass u_i dissimilating as a result of interaction of plants which have biomasses u_i and u_j, $Q_i(t,x)$ is the influence of competitive interaction upon dissimilation. (We may note that by $i = j$ intraspecific competition takes place, whereas by $i \neq j$ interspecific competition appears).

The main result of modeling with the aid of integral approach consists in obtaining effects of heterogeneity (spotty areas) in the spatial distribution of plants under homogeneous and stationary external conditions. When modelling miltispecies associations, it turned out well to account for effect of space dividing into habitats of different species. To be more precise, the achieved results may be formulated as follows. If intraspecific competition exceeds interspecific one the species get mixed up in the space and coexist in a stable manner, the limit distribution not depending on the initial conditions. Initial conditions influence the character of spotty areas (shape of spots) (in case of their availability) and the spatial distribution of biomass for different species. If interspecific competition exceeds intraspecific one species seek to divide the space into habitats. The considerable areas of space come into being where one species is ousted by the other, and location of the dividing boundaries is determined by initial conditions. Boundary shapes are also

studied within this model. Its shortcomings may be regarded as the extension of model's advantages. In view of the bulky structure of this model, it's possible to obtain concrete results only with the aid of numerical methods.

In many works (Komarov, 1985, Galitsky et al., Grabarnik, Komarov 1981) spatio-temporal dynamics of plant associations is retraced numerically, with the aid of models representing properly constructed Markovian process. Though these models are virtually not ecophysiological ones, they allow, however, to retrace forming of the spatial images (patterns) referring to sizes of individual trees depending on types of the introduced competitive interaction. In this connection, it would be interesting to dwell on the work by Galitsky and Krylov (1985). Within the framework of developed model, biomass of each plant located within own cell changes, in accordance with the law defined by equation (2.22), till either the given plant or its neighbour dies off because of the deficiency in territory. At the moment of dying-off, it takes place, strictly speaking, interaction of plants in the form of "sharing" of area which has become free because of the death of the given plant. As the separate plants die off, it takes place changing of the initial mosaic corresponding to initial sizes of plants. Even taking into account essential simplicity of this model, there are many versions of the geometrical structure of system (composed of the individual elements) against the background of possible variations of model parameters.

There are some versions of synthesizing this approach and the integral one (Galitsky, Tuzinkevich, 1987). In particular, it was shown in these works that stochastic approach to the model describing competitive interactions of plants is very fruitful for interpretation of growth dynamics for plants growing within association. Furthermore, it was proved, at the model level, that the initial almost homogeneous spatial structure of association becomes altered in the course of its development and gains spotty character.

CONCLUSION

Within the framework of the present survey, one of the directions in modeling of forest stand dynamics is considered, namely ecophysiological "explaining" models, both analytical and simulative ones. This survey doesn't claim to be a complete one since not all works are reviewed and a number of significant aspects of modeling are not considered. Among them, we can mention the question concerning problems and methods of identification of models that is necessary both for their practical application in the task of forecasting, monitoring, etc., and for the analysis of critical conditions of object functioning, as well as for describing of spatial boundaries.

The next logical steps (proposed mainly by the last of the co-authors) in improving the simulation capabilities of the boreal models are several-fold, but in many cases could be attacked simultaneously. In no particular order, these steps include:

1. Improved characterization of soil surface features and surface dynamics. The nature of the ground surface can have a fairly profound effect on the heat transfer to and from the boreal soils and the associated temperature effects are important with respect to any number of processes. The dynamics of moss, lichen and litter layers in the forests are extremely important and an increased knowledge-base is important.

2. Increased understanding of feedbacks in biogeochemical cycles. Several of the chapters have touched upon the importance of nutrients in understanding the dynamics of boreal forests. Chapter 8 and nutrient-cycling forest simulation models (Pastor and Post 1986, 1988) point to the possibility of multiple-stable equilibria in the southern transition between boreal and temperate deciduous forests. The understanding of the effects of

nutrient availability on tree growth and/or form for a variety of species would be an important addition.

3. Coupling of more explicit plant physiology into the stand simulation models. Using plant physiology (particularly leaf level responses typically resolved at time scales of minutes) to predict the annual growth of trees has been pursued for several decades. The linking of canopy models that incorporate a considerable degree of fundamental plant physiology to stand simulation models appears to be an attainable objective at this time. The interaction between the two models is in both directions. Canopy physiology models attempt to represent fundamental biophysical processes (or reasonable proxies thereof) to predict the carbon fixation of a layered, horizontally homogeneous canopy. The models can provide an estimate of total carbon fixed by a canopy over a period of time but (because they represent the forest as a homogeneous, aggregated system) they have no internal features to alter canopy structure over time. Stand simulation models would be improved by the addition of total productivity and because they grow individual trees based on indices that include competition and other factors can deallocate a given degree of productivity into tree growth and canopy dynamics. The assessment of the direct effects of increased ambient CO_2 in the atmosphere will probably continue to make the interfacing of plant physiological models and stand dynamics models an important topic.

4. An increased ability to observe large scale pattern. The feedback dynamics that have emerged in many of the preceding chapters in many cases imply patterns on the boreal landscape. Remote sensing offers an important family of methodologies for

detecting such pattern -- particularly for ecosystems like the boreal forests in which large tracts of the forest are relatively inaccessible.

5. **Basic studies to connect the surface features of the boreal forests to other geospheric systems, particularly the atmosphere.** The annual variation in the CO_2 concentration by latitude is greatest in the higher northern latitudes and appears to be well correlated with the uptake of photosynthetically active radiation in boreal regions. The role of the worlds boreal forests as major terrestrial repositories of carbon, the importance of the carbon cycle, and our need to better understand global carbon dynamics all point to a need for a better understanding of the interaction between the forest surface in boreal zones and the atmosphere. The hopeful scenario is for these studies (some of which are being drafted currently) to also provide valuable data for step 3 (above).

6. **Testing and application of the models over large areas and over long time scales.** The model testing step hopefully will provide some appreciation of the potential applications of the models and of the next information needed. It is our hope that by making the models available to our colleagues that this testing over large areas will take us to a next step in ordering research needs. Tests over long time scales with these models will likely be retrospective simulations developed in conjunction with paleoecological studies.

7. **Incorporation of animal-plant interactions with vegetation dynamics models.** Insects can have a particularly significant effect on boreal forest dynamics. Also there are several

important interactions among forest composition, element cycles and large herbivore grazing. Clearly there are major feedback systems involving animals. The animal-involved interactions with boreal forest ecosystems appear to be able to change the spatial grain, the dynamics and the stability of boreal forests.

8. _Continued_ _effort_ _in_ _coupling_ _of_ _wildfire_ _dynamics_ _and_ _forest_ _dynamics_ _in_ _boreal_ _models._ The importance of wildfire in shaping the forests of the boreal zone has been discussed in several reviews, and there has been a considerable effort in the modeling of the vegetation/wildfire interaction. The ecology of the boreal forest is so shaped by fire and the fire has such a regular presence on the boreal landscape that continued work to improve our knowledge base and the representation of fire in models is imperative. From a modeling stand-point, consideration of fire has several important aspects namely the fire initiation and spatial propagation, and the coupling of tree-level phenomena with landscape-level wildfire behavior, the quantification of boreal fires as CO, CO_2 and other organic compounds sources to the atmosphere.

LITERATURE CITED

Agreen, G.I., Axelsson, B.   PT - a tree growth model.   In:
Ecological Bulletins, 32, Stockholm, 1980, pp. 525-536.

Antonovsky, M.Ya., Korzukhin, M.D., Mathematical modeling of
economical and ecological-economical processes.   In: The
comprehensive global monitoring of environmental state.
Tbilisi, 1983, pp. 353-358 (in Russian).

Antonovsky, M.Ya., Korzukhin, M.D.   Hierarchic modeling of
plant dynamics by predicting the biosphere state.   In: The
comprehensive global monitoring of biosphere state.
Proceedings of the 3rd International Symposium, 1986, vol. 2,
pp. 71-80 (in Russian).

Antonovsky, M.Ya., Kuznetsov, Y.A., Fleming, R.A.   The
reaction of conifer forest to pest invasion: the simplest
dynamical model.   In: Problems of ecological monitoring and
ecosystem modeling.   Leningrad: Hydrometeoizdat, 1988, vol. 2,
pp. 160-168 (in Russian).

Antonovsky, M.Ya., Aponina E.A., Kuznetsov, Yu.A.   Spatial-
temporal structure of mixed-age forest boundary: the simplest
mathematical model.   WP-89-54, 1989, IIASA, Laxenburg,
Austria.

Bazykin, A.D.   Mathematical biophysics of interacting
populations.   Moscow: Nauka, 1985, 181 p. (in Russian).

Bazykin, A.D., Kuznetsov, Y.A., Khibnik, A.I.   Bifurcation
diagrams of dynamical systems located on the plane.
Information issue.   Pushchino: ONTI NCBI AN SSSR, 1985 (in
Russian).

Berezovskaya, F.S., Karev, G.P.   Conception of spatio-temporal
measure structure ad modeling of stand dynamics.   In:
Proceedings of International Symposium "Boreal forests: state,
dynamics, anthropogenic influence", 1990, part 3, pp. 3-11 (in
Russian).

Bertalanffy, L.   Theoretische Biologie.   Berlin-Zenlendorf:
Borntraeger, 1942, XVI, 302 p.

Bikhele, Z.N., Moldau, H.A., Ross, Y.K.   Mathematical modeling
of transpiration and plant photosynthesis by deficiency of the
soil moisture.   Leningrad: Hydrometeoizdat, 1980, 223 p. (in
Russian).

Bogatyrev, B.G.   Modeling of transient processes at the
boundary between plant zones by anthropogenic changes of
climate (for the particular system tundra-taiga).
Dissertation for the degree of candidate of physico-
mathematical sciences.   Moscow, 1988 (in Russian).

Bogatyrev, B.G. Kirilenko, A.P., Tarko, A.M. Spatially distributed models of biosphere. Moscow: Computer Centre of AN SSSR, 1988, 23 p. (in Russian).

Bonan, B.G. A computer model of the solar radiation, soil moisture and soil thermal regimes in boreal forests. Ecological Modelling, 45, 1989, pp. 275-306.

Bonan, B.G. A listing of the biophysical configuration of the BOFORS (Version 1b) model. Science and Technology Library, The University of Virginia, Charlottesville, Virginia, 1990.

Bormann, F.H., Likens, G.E. Pattern and process in a forested ecosystem. Springer-Verlag, N.Y., 1979, 253 pp.

Botkin, D.B., Janak, J.F., Wallis, J.R. The rationale, limitations and assumptions of north-east forest growth simulator. ISM, J. Res. Development, 1972, 1G, pp. 101-116.

Boulange, E.N. Analysis of the model describing the development of forest population under the influence of pests. Vestnik MGU, series 15 (Computing mathematics and cybernetics), 1984, 4, pp. 36-41 (in Russian).

Burgovsky, V.V., Dudin, E.B., Mellina, E.G. Tselniker, Y.L. Modeling of productional processes within prize stands. Zhurnal obshehry biologii, 1982, 43(4), pp. 450-455 (in Russian).

Burgovsky, V.V. Lintov, L.I. Mellina, E.G. Modelling of stand development by taking into account climate conditions. Zhurnal obshehry biologii, 1987, 45(1), pp. 84-91 (in Russian).

Buzykin, A.I., Sekretenko, O.P., Khlebopros, R.G. Structure of arboreal cenoses. In: Readings in commemoration of V.I. Sukachev, part 5. Moscow: Nauka, 1987 (in Russian).

Cherkashin, A.K. Model of spatial-age structure of forest. In: Models for management of natural resources. Moscow: Nauka, 1981, pp. 231-242 (in Russian).

Chetverikov, A.N. Comparative analysis of three models describing respiration of plants. Fiziologia resteniy, 1985, 32(3), pp. 432-439 (in Russian).

Computers and mathematics with applications, vol. 9, 3, 1983.

Cowan, I.R. Regulation of water use in relation to carbon gain in higher plants. In: Lange, O.L., Noble, P.S., Osmond, C.B., Ziegler, H. (eds.), Physiological plant ecology. Encycl. Plant Physiol. (NS). Springer Berlin, 1982, vol. 12B, pp. 549-587.

Cowan, I.R. Economics of carbon fixation in higher plants. In: Givnish, I.J. (ed.), On the economy of plant form and function. Cambridge Univ. Press, Cambridge, 1986, pp. 133-170.

Elton, C. Animal ecology. Macmillan, New York, 1927.

Emanuel, W.R., Killough, G.G., Post, W.M., Shugart, H.H. Modeling terrestrial ecosystems and the global carbon cycle with shifts in carbon storage capacity by land use change. Ecology, 1984, 65, pp. 970-983.

Emanuel, W.R., Fung I.Y-S., Killough, G.G., Moore, B., Peng, P.H. Modeling the global carbon cycle and changes in the atmosphere CO_2 levels. In: Trabalka, J.R. (ed.), Atmospheric CO_2 and the global carbon cycle. Carbon Dioxide Research Division, US-DOE, Washington, D.C., 1985, pp. 141-173.

Ericsson, A. Effects of fertilization and irrigation on the seasonal changes of carbohydrate reserves in different age-classes of needle on 20-year-old Scots pine trees. Physiol. Plant, 1979, 45, pp. 270-280.

Farquhar, G.D., von Caemmer, S. Modeling of photosynthetic response to environmental conditions. In: Lange, O.L., Noble, P.S., Osmond, C.B., Ziegler, H. (eds.), Physiological plant ecology. Encycl. Plant Physiol. (NS). Springer, Berlin, 1982, vol. 12B, pp. 549-587.

Farquhar, G.D., Sharkey, T.D. Stomatal conductance and photosynthesis. Annual Review of Plant Physiology, 1982, 33, pp. 317-345.

Fries, J. (ed.). Growth models for tree and stand simulation. Dept. of forest yield research. Res. Notes, 30, Stockholm, 1974.

Galitsky, V.V. Dynamic 2-D MODEL of plant communities. J. Ecological Modelling, 50, 1990, pp. 95-105.

Galitsky, V.V. Komarov, A.S. On non-free growth of the organism biomass. Pre-print. Pushchino: ONTI NCBI AN SSSR, 1978, 21 p. (in Russian).

Galitsky, V.V., Krylov, A.A. Numerical modeling of dynamics for even-aged plant association. Two-dimensional model. In: Mathematical modeling in biogeocenolgy. Petrozarvolsk, 1985, pp. 61-62 (in Russian).

Galitsky, V.V. Tuzinkevich, A.V. About one approach to modeling of the experimental homogenous plant associations. Pre-print. Pushchino: ONTI NCBI AN SSSR, 1987, 11 p. (in Russian).

Gavrikov, V.L. Age dynamics for tree populations. In: Analysis of structure of arboreal cenoses. Novosibirsk, 1985, pp. 50-70 (in Russian).

Gorben, A.N. Sadovsky, M.G. Optimization models of migration: globally informed individuals. In: Problems of ecological monitoring and ecosystem modeling. Leningrad: Hydrometeoizdat, 1988, vol. 2, pp. 186-197 (in Russian).

Grabarnik, P.Ya. Probabilistic model describing spatial structure of stand by taking into account three sizes. In: Theses of reports made in the conference "Ecology of populations". Novosibirsk, 1988, pp. 15-20 (in Russian).

Grabarnik, P.Ya., Komarov, A.S. Statistical analysis of horizontal structure of stands. In: Modeling of biogeocenosis processes. Moscow: Nauka, 1981, pp. 119-135 (in Russian).

Gurtin, M.E., MacCamy, R.C. Non-linear age-dependent population dynamics. Arch. Rat. Mech. Anal., 3, 1974, pp. 281-300.

Gurtsev, A.I., Korzukhin, M.D. Crown and root competition by line planting of pine. In: Problems of ecological monitoring and ecosystem modeling. Leningrad: Hydrometeoizdat, 1988, vol. 2, pp. 206-223 (in Russian).

Hilderman Y.I., Kudrina, K.N., Poletayev, I.A. Models of Λ-systems (systems with limiting factors). In: Cybernetical researches. Moscow: Sovetskrye radio, 1970, pp. 165-210 (in Russian).

Hilmi, G.F. Theoretical forest biolgeophysics. Moscow, AN SSSR, 1957, 295 p. (in Russian).

Hilmi, G.F. Energetics and productivity of plant cover. Leningrad: Hydrometeoizdat, 1976, 215 p. (in Russian).

Himmelfarb, A.A., Ginzburg, L.R., Poluektov, F.V., Pykh, Y.A., Ratner, V.A. Dynamic theory of biological populations. Moscow: Nauka, 1974, 456 p. (in Russian).

Huxley, J.S. Problems of relative growth. New York: Diul Press, 1932, 296 p.

Insarov, G.E. Alternation of growth and reproduction within ontogeny. In: Energetical aspects in growth and reproduction of invertebrates. Minsk, 1975, pp. 23-29 (in Russian).

Janseitov, K.K., Kuzmichev, V.V. Forming of mosaic structure in stands. In: Research of dynamics of organism growth. Novosibirsk: Nauka, 1981, pp. 78-86 (in Russian).

Kareiva, P., Andersen, M. Spatial aspects of species interactions: The wedding of models and experiments. In: Hastings, A. (ed.), Community Ecology, Lecture Notes in Biomathematics 77, Springer-Verlag, Berlin, 1988, pp. 35-50.

Karev, G.P. Asymptotic behavior of population models with age and inner structures. In: Mathematics and modeling. Pushchino, 1990, pp. 238-254 (in Russian).

Karev, G.P. Dynamics and asymptotic behavior of models describing structural populations. In: Modeling of processes of ecological development. Collected proceedings of VNIISI, No. 12. Moscow, 1987, pp. 82-94 (in Russian).

Karev, G.P. Mathematical model of competing for light within light-limited self-thinning stands. Zhurnal obshehry biologii, 1985a, vol. 46, 1, pp. 114-123 (in Russian).

Karev, G.P. On modeling of multispecies phytocenoses. In: Problems of ecological monitoring and ecosystem modeling. Leningrad: Hydrometeoizdat, 1985b, vol. 7, pp. 227-233 (in Russian).

Karev, G.P. On mathematical models of stand growth. In: Promising phytocenological theories. Tartu, 1988, pp. 198-203 (in Russian).

Karev, G.P. On one approach to modeling of stand growth. In: Mathematical biophysics. Krasnoyarsk, 1985, pp. 161-167 (in Russian).

Karev, G.P. Representation of solutions for some non-linear models of structural populations. In: Mathematical modeling in problems of rational nature use. Tostov-a-Donu, 1989, pp. 69-70 (in Russian).

Karev, G.P., Treskov, S.A. Mathematical models of boundary object within phytocenoses. In: Problems of ecological monitoring and ecosystem modeling. Leningrad: Hydrometeoizdat, 1982, vol. 5, pp. 229-242 (in Russian).

Katayeva, K.V., Korzukhin, M.D. Dynamics of cedar forests with dark needles. Moscow, 1987, 115 p. (in Russian).
Kofman, G.V. Biological significance of allometric relations. In: Research of dynamics of organism growth. Novosibirsk: Nauka, 1981, pp. 31-55 (in Russian).

Kofman, G.V., Kuzmichev, V.V., Khlebopros, R.G. Utilization of stand growth parameters for the tasks of classification. In: Mathematical analysis of components of forest biogeocenoses. Novosibirsk: Nauka, 1979, pp. 5-24 (in Russian).

Komarov, A.S. Computational experiment by research of populations concerted of vegetatively mobile herbaceous plats. In: Mathematical modeling of biogeocenosis processes. Moscow: Nauka, 1985, pp. 70-79 (in Russian).

Korzukhin, M.D. Age dynamics for populations of trees being strong edificators. In: Problems of ecological monitoring and ecosystem modeling. Leningrad: Hydrometeoizdat, 1980, vol. 3, pp. 162-178 (in Russian).

Korzukhin, M.D. Changes of productivity and numbers for two-species succession by variations of growth behavior. Ibidem, 1985a, vol. 8, pp. 207-219 (in Russian).

Korzukhin, M.D. On ecophysiological model of forest dynamics. Ibidem, 1986, vol. 9, pp. 259-276 (in Russian).

Korzukhin, M.D. Some strategies of plant ontogeny under competitive conditions. Ibidem, 1985a, vol. 7, pp. 234-241 (in Russian).

Korzukhin, M.D. Comparative assessment of modeling methods in the forest dynamics. In: Soviet-Mongolian experiment UBSU-NUR. Thesis. Pushchino, 1989, pp. 75-79 (in Russian).

Korzukhin, M.D. Matskiavichus, V.K., Antonovsky, M.Ya. Periodic behavior of age-distributed tree population. In: Problems of ecological monitoring and ecosystem modeling. Leningrad: Hydrometeoizdat, 1989, vol. 12, pp. 284-390 (in Russian).

Korzukhin, M.D., Sedykh, V.A. On background monitoring of forests in the West Siberia. Ibidem, 1983, vol. 6, pp.232-130 (in Russian).

Korzukhin, M.D. Sedykh, V.A., Ter-Mikhaelyan, M.T. Formulation of the predicting model describing age-recreative dynamics of forests. Irv. SO AN SSSR, biol., 1099, 1(5), pp. 57-69 (in Russian).

Korzukhin, M.D., Ter-Mikhaelyan, M.T. Competing for light and dynamics of modeled individuals which are distributed independently on a plane. In: Problems of ecological monitoring and ecosystem modeling. Leningrad: Hydrometeoizdat, 1982, vol. 5, pp. 242-248 (in Russian).

Korzukhin, M.D., Ter-Mikhaelyan, M.T. Optimum ontogeny of plants by taking into account protection and competition. Ibidem, 1987, vol. 10, pp. 244-256 (in Russian).

Kudrina, K.N. Mathematical model of higher plant. In: Physiological adaptation of growth to field conditions. Novosibirsk: Nauka, 1973, pp. 25-57 (in Russian).

Kull, K.L. Development and analysis of ecophysiological model describing growth of a whole tree (for a particular case of fir). Dissertation for the degree of candidate of biological sciences. Tarta, 1986 (in Russian).

Kull, K.L., Kull, O. Dynamical modeling of tree growth. Tallinn: Valgus, 1989, 232 p. (in Russian).

Kull, K.L., Ora, T.A. Structure of physiological models describing tree growth. Irv. HN SSSR, Biologia, 1984, 33(2), pp. 33-41 (in Russian).

Kuzmichev, V.V. Essential features of stand growth. Novosibirsk: Nauka, 1977, 112 p. (in Russian).

Leak, W.B. Successional change in north hardwoods predicted by birth and death simulation. Ecology, 1970, 51(5), pp. 794-801.

Lediy, F.T. A growth model for the seedlings based upon the rate of photosynthesis and the distribution of photosynthete. Photosynthetica, 1969, vol. 3, n. 3, pp. 263-275.

Leemans, R. A listing of the biological configuration of the BOFORS (Version 1a) model. Science and Technology Library, The University of Virginia, Charlottesville, Virginia, 1990.

Leemans, R., Prentice, F. FORSKA a general forest succession model. Meddel. fraan växt. biol. instit., 2, Uppsala, 1989.

Leslie, P.H. On the use of matrices in certain population mathematics. Biometrika, 45, vol. 33(3), pp. 183-212.

Liebig, I. Die Grundsätze der Agrikultur-Chemie, Brunnswick, 1985.

Lindeman, R.L. The trophic-dynamic aspect of ecology. Ecology, 1942, 23, pp. 399-418.

Logofet, D.O. On the qualitative stability of ecosystems. Zhurnal obshehry biologii, 1978, 39(6), pp. 817-822 (in Russian).

Lotka, A. Elements of physical biology. Williams and Wilkins, 1925, 460 p.

MacArthur, R.H. Species packing and competitive equilibrium for many species. Theor. Pop. Biol., 1970, 1(1), pp. 1-11.

McCree, K.J. Equation for the rate of respiration of white clover plants grown under controlled conditions. In: Prediction and measurement of photosynthetic productivity. Wageningen: Pudoc, 1970, pp. 221-229.

McMurtrie, R. A plant-water model with implications for the management of water catchments. Lecture Notes in Biomathematics, 1981, 40, pp. 206-224.

Molchanov, A.M. Ecology and ergodieity. In: Simulative modeling and ecology. Moscow: Nauka, 1975, pp. 49-55 (in Russian).

Moldau, H. Model of plant productivity at limited water supply considering adaptation. Photosynthetica, 1971, 5(1), pp. 16-21.

Moldau, H.A. Autoregulation of production process of plants in case of water deficiency. Author's abstract of dissertation for the degree of doctor of biological sciences. Moscow, 1984, 44 p. (in Russian).

Monsi, M., Saeki, T. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jap. J. Bot., 1953, vol. 14, pp. 22-52.

Moskalenka, H.I., Cherkshin, A.K. Modeling of the system "forest-river" from the standpoint of management tasks. In: Dynamics of ecological-economical systems. Novosibirsk: Nauka, 1981, pp. 92-107 (in Russian).

Nilson, T. Theory of radiation passing through the homogenous plant cover. In: Passing of solar radiation through a plant cover. Tartu: IAF AN SSSR, 1977, pp. 5-70 (in Russian).

Odum, E.P. The strategy of ecosystem development. Science, 1969, 164, pp. 262-270.

Oja, T. Models of stand development. Tartu, 1985a, 60 p. (in Russian).

Oja, T. On spatial and temporal changeability of stand structure (in a specific case of fir stands). Dissertation for degree of candidate of biological sciences. Tartu, 1984 (in Russian).

Oja, T. Simple adaptive model of plant. 1. Description of the model. Irv. AN SSSR, Biologica, 1985b, 34(4), pp. 289-294 (in Russian).

Oja, T. Simple adaptive model of plant. 2. Analysis of the model. Ibidem, 1986, 35(2), pp. 16-29 (in Russian).

Oster, G. Lectures in population dynamics. In: Lectures in Appl. Math., vol. 16, Providence, 1977.

Plotnikov, V.V. Evolution of structure of plant association. Moscow: Nauka, 1979, 276 p. (in Russian).

Poletayev, I.A. On mathematical models of growth. In: Physiology of adaptation of plants to soil conditions. Novosibirsk: Nauka, 1973, pp. 7-24 (in Russian).

Poletayev, I.A. On mathematical models of elementary processes in biogeocenoses, In: Problems of cybernetics. Moscow, 1966, N 16, pp. 171-190 (in Russian).

Poluektov, R.A., Pykh, Y.A., Shvybov, I.A. Dynamical models of ecological systems. Leningrad: Hydrometeoizdat, 1980, 255 p. (in Russian).

Promnitz, L.C. A photosynthate allocation model for tree growth. Photosynthetica, 1975, 9(1), pp. 1-15.

Rachko, P. Simulative model of growth dynamics for a tree as element of forest biocenosis. In: Problems of cybernetics. Moscow, 1979, part 52, pp. 73-111 (in Russian).

Rachko, P. Simulative model of tree growth: construction of model. Zhurnal obshehry biologii, 1978, 39(4), pp. 563-571 (in Russian).

Razzhervaikin, V.N. Spatially distributed two-level ecosystems. In: Mathematical methods in ecology and genetics. Moscow: Nauka, 1981, pp. 36-50 (in Russian).

Reynolds, J.F. Bachelet, D., Leadley, P., Moorhead, D. Response of vegetation to carbon dioxide. Assessing the effects of elevated carbon dioxide on plants: toward the development of a generic plant growth model. Progress Report 023 to U.S. Dept. of Energy, 1986.

Robertson, T.B. The chemical basis of growth and senescence. London: J.B. Lippincott, 1923, 389 p.

Ross, Y.K. Radiation conditions and architectures of plant cover. Leningrad: Hydrometeoizdat, 1975, 342 p. (in Russian).

Running, S.W., Coughlan, J.C. A general model of forest ecosystem processes for regional applications I. Hydrological balance, canopy gas exchange and primary production processes. Ecological Modeling, 1988, 42, pp. 125-154.

Samarskaya, E.A. Forest-pest interaction dynamics in temporal and spatial domains. WP-89-16, 1989, IIASA, Laxenburg, Austria.

Schmalhausen, I.I. Growth and differentiation. Kiev: Naukova dumka, 1984, vol. 2, 168 p. (in Russian).

Semevsky, F.M., Semenov, S.M. Mathematical modeling of ecological process. Leningrad: Hydrometeoizdat, 1982, 280 p. (in Russian).

Shinozaki, K., Yoda, K. Hozumi, K., Kira, T. A quantitative analysis of plant form - the pipe model theory. Jap. J. Ecol., 1964, 14, pp. 97-105.

Sholokhov, A.G. Modeling of density dynamics for beech stands growing in the Norther Caucasus. Dissertation for the degree of candidate of agricultural sciences. Moscow, 1990 (in Russian).

Shugart, H.H. Theory of forest dynamics. The ecological implications for forest succession models. N.J.: Springer, 1984, XTV, 278 p.

Shugart, H.H., Crow, T.R., Hett, J.M. Forest succession models: a rationale and methodology for modelling forest succession over large region. Forest Sci., 1973, 19(3), pp. 203-212.

Shugart, H.H., Emanuel W.R., West, D.C., Deangelis, D.L. Environmental gradients in simulation model of a beech-yellow-poplar stand. Math. Biosci., 1980a, 50(3-4), pp. 163-170.

Shugart, H.H., Goldstein, R.A., O'Neill, R.V., Mankin, J.B. TEEM: a terrestrial ecosystem energy model for forests. Decologia Plantarum, 1974, 9(3), pp. 231-264.

Shugart, H.H., Hopkins, M.S., Burgess, I.P., Nortlock, A.T. The development of succession model for subtropical rain forest and its application to access the effects of timber harvest at Wiangaree State Forest, New South Wales. J. Environ. Manag., 1980b, 11(3), p. 243-265.

Shugart, H.H., Noble, I.R. A computer model of succession and fire response of the high altitude Eucalyptus forests of the Brindabella Range, Australian capital territories. Austr. J. Ecol., 1980.

Shugart, H.H., West, D.C. Development of an Appalachian deciduous forest succession model and its application to assessment of the chestnut blight. J. Environ. Management, 1977, 5, pp. 161-179.

Shugart, H.H., Antonovsky, M.Ya., Jarvis, P.G., Sandford, A.P. CO_2, climatic change and forest ecosystems: Assessing the response of global forests to the direct effects of increasing CO_2 and climatic change. In: Bolin, B., Döös, B.R., Jäger, J, Warrick, R.A. (eds.), The greenhouse effect, climatic change and ecosystems (SCOPE 29). John Wiley, New York, 1986, pp. 475-521.

Shvidenko, H.Z. Theoretical ad experimental foundations of inventory system for mountain forests within zone of intensive forest management. Author's abstract of dissertation for the degree of doctor of agricultural sciences. Kiev, 1981, 38 p. (in Russian).

Sitorin, A.P. Diffusive approach to models describing dynamics of populations and biological associations. In: Mathematical models in ecology and genetics. Moscow: Nauka, 1981, pp. 51-71 (in Russian).

Smirnova, O.V., Chistiakova, A.A., Popaduik, R.V., Evstigneyev, L.I., Korotkov, V.N., Mitrofanova, M.V. Ponomarekho, E.V. Population organization of plant cover of forest territories in specific case of broad-leaved forests in the European part of the USSR. Information edition. Pushchino, 1990, 92 p. (in Russian).

Sokolov, E.E., Puzachenko, Y.G. Foundations of general scheme for allocation of elements of global monitoring network and biosphere reservations areas. In: The comprehensive global monitoring of biosphere state. Proceedings of the 3rd International Symposium, 1986, vol. 2, pp. 20-26 (in Russian).

Sollins, P., Harris, W.F., Edwards, N.T. Simulating the physiology of deciduous forest. In: System analysis and simulation in ecology. New York, 1976, pp. 173-218.

Surchanov, V.V. Model of species structure for plant association under conditions of variable environment. In: Empirical research methods and modeling of plant associations. Vladivostok, 1988, pp. 51-70 (in Russian).

Svirezkev, Y.M., Elizarov, E.Ya. Mathematical modeling of ecological systems. In: Problems of space biology. Moscow: Nauka, 1972, vol. 20 (in Russian).

Svirezkev, Y.M., Logofet, D.O. Stability of biological associations. Moscow: Nauka, 1978, 153 p. (in Russian).

Ter-Mikhaelyan, M.T., Furiayev, V.V. Model of spatio-temporal dynamics of forests under the influence of fires. In: Problems of ecological monitoring and ecosystem modeling. Leningrad: Hydrometeoizdat, 1988, vol. 2, pp. 260-275 (in Russian).

Terskov, I.A. Terskova, M.I. Growth of even-aged stands. Novosibirsk: Nauka, 1980, 206 p. (in Russian).

Thornley, J.H.M. Respiration, growth and maintenance in plants. Nature, 1970, 227(5255), pp. 304-305.

Thornley, J.H.M. Mathematical models in plant physiology. London: Academic Press, 1976, XVI, 318 p.

Thornley, J.H.M. Mathematical models in plant physiology. Kiev: Naukova dumka, 1982, 321 p. (in Russian).

Tillman, D. Plant strategies and dynamics and structure of plant communities. Princeton Univ. Press, Princeton, 1988.

Tooming, H.G. Solar radiation and development of crops. Leningrad: Hydrometeoizdat, 1977, 200 p. (in Russian).

Tselmkev, Y.L. Functional and structural organization of photosynthetic apparatus of forest wood plants. In: Ecophysiological researches of photosynthesis and water conditions in the field. Irkutsk, 1983, pp.5-15 (in Russian).

Tucker, S.L., Zimmerman, S.O. A nonlinear model of population dynamics containing an arbitrary number of continuous structure variable. SIAM J. Appl. Math., 1988, 48(3).

Tuzinkevich, A.V. Mathematic modeling of spatio-temporal dynamics of biological systems with the aid of integro-differential equations. Dissertation for the degree of candidate of physico-mathematical sciences. Vladivostok, 1987 (in Russian).

Tuzinkevich, A.V. Frisman, E.Ya. On a model of spatial distribution of biological association. In: Empirical research methods and modeling of plant associations. Vladivostok, 1988, pp. 71-89 (in Russian).

Volterra, V. Lecons sur la theorie mathematique de la lutte pour la vie. Paris, 1931.

Watt, A.S. Pattern and process in the plant community. Journal of Ecology, 1947, 35, pp. 1-22.

Weatherhead, P.J. How unusual are unusual events? American Naturalist, 1986, 128, pp. 150-154.

Webb, G.F. Dynamics of population structured by internal variables. Math. Zeitschrift, 189, n. 3, 1985.

Whittaker, R.H., Levin, S.I. The role of mosaic phenomena in natural communities. Theor. Popul. Biol., 1977, 12, pp. 117-139.

Zorotyntsev, A.V. Utilization of optimum principle to describe growth functions on the models of plant growth. In: Mathematical modeling in biogeocenology. Petrozavodsk, 1985, pp. 108-110 (in Russian).