WORKING PAPER

PREDICTIVE FOREST ECOSYSTEM MODELS AND
IMPLICATIONS FOR INTEGRATED MONITORING

M.Ya. Antonovsky
M.D. Korzukhin

IIASA

International Institute
for Applied Systems Analysis

PREDICTIVE FOREST ECOSYSTEM MODELS AND IMPLICATIONS FOR INTEGRATED MONITORING

M.Ya. Antonovsky
M.D. Korzukhin

FOREWORD

For many years Soviet scientists have provided leadership in the design of integrated environmental monitoring system. The attached paper by M.Ja. Antonovsky and M.D. Korzukhin is a good example of the approach taken, in which a working ecological model is developed and then applied to the practical problem of designing an appropriate environmental monitoring system.

The paper was presented at a Symposium held in Moscow 13–16 March, 1985, cosponsored by IIASA and the USSR National Committee for IIASA. During the same week a Memorandum of Agreement was drafted and subsequently signed by Academician Yu.A. Izrael and Dr. T. Lee, assuring Soviet collaboration in the IIASA Project, "Ecologically Sustainable Development of the Biosphere".

One outcome of the Memorandum is the arrival of Professor Antonovsky at IIASA in May 1986. In his capacity as Chief Scientist in the Environment Program, Dr. Antonovsky will continue his research in the fields of ecological modeling and the design of integrated monitoring systems.

R.E. Munn
Head, ENV Program

SUMMARY

This work is devoted to a method of modeling forest ecosystem dynamics that can be used in integrated global monitoring of the biosphere. As is well known, attempts to calculate global (or regional, zonal, etc.) variation of, for example, forest productivity under varying global temperature but with an average warming trend with corresponding variations in productivity of a single tree and a number of trees in a given territory will never be successful: the result will be quantitatively incorrect even with respect to sign, because the multilevel forest structure and a great number of possible impacts of temperature on forest ecosystem are not taken into account. Indeed, CO_2 growth stimulation in a fixed density stand first leads to an increase in the accumulated biomass and then to a reduction, because of competitive mortality (at the individual and group levels). The associated drying up and reduction of the area of swamps, at the same time, stimulates fires, thus shortening the average age of forests. On the whole, forest biomass, despite an increase in area, may either increase or decrease (at the landscape and regional levels). For territories with low temperature, warming will stimulate individual growth, further reducing the biomass at the fitocenous level as well as at the landscape level due to the stimulation by fire and phytophagas; the net effect of these variations may be either positive or negative.

Generally speaking, we use a well-known approach, viz., from a concrete natural problem to a hierarchy of mathematical models, followed by a computing experiment and interpretation of the result. The complexity of a model has to correspond to the study goal, the preciseness of experimental data, the level of detail of existing methods and algorithms.

Past experience has shown that many complex nonlinear phenomena could be prescribed with the aid of relatively simple models. See, for example, the work of A. Turing on modeling of morphogenesis and analogous modeling of chemical reactions by I. Prigogin.

We wish to express our appreciation and gratitude to Professor R.E. Munn, Leader, Environment Program at IIASA, for his suggestions.

PREDICTIVE FOREST ECOSYSTEM MODELS AND IMPLICATIONS FOR INTEGRATED MONITORING

M.Ya. Antonovsky* and M.D. Korzukhin**

It is convenient to divide the factors influencing the state of an ecosystem into those directly affecting it ("local", or explicit ones), and indirect ones, whose effects depend on the state of adjacent ecosystems ("terrirotial" factors, with implicit effects).

In the following analysis, we shall discuss forest ecology of the taiga zone. The local factors of importance are as follows: microclimate, bogging, forest pests, other biotic factors and windfalls. Regional factors include: forest fires, bogging, regional-scale pest outbreaks and other biotic factors (birds, fungus diseases) [24].

In accordance with this view, there are two aspects to predictions of changes in the state of the taiga forests under hypothesized climate variations or physico-chemical changes in the atmosphere:

---

*Currently Chief Scientist in the Environment Program at IIASA.

**Natural Environment and Climate Monitoring Laboratory GOSKOMGIDROMET, Moscow.

1. It is necessary to predict the direct ecological impacts due to changes in externalities, i.e. to assess changes in biomass, the number of trees, etc. Taking into account the fact that there are strong ecological effects due to competition in the boreal forests [20], the response of the ecosystem as a whole would not be, generally speaking, the sum total of responses observed in the case of non-interacting individuals. An adequate ecological model is essential in order to predict the response of the total system.

2. It is also necessary to predict indirect ecological impacts due to large-scale changes in externalities. These predictions are obtained from measurements and models of ecological structural changes within each vegetation zone. A region is conceived as a "mosaic" of a multitude of ecosystems existing in various habitats and at different successional stages. In the case of the taiga forest, this mosaic is largely due to fire [11]. Here it should be noted that methods for modelling ecosystem dynamics are relatively developed; however, our understanding of ecosystem structural changes over large regions is still relatively poor, and only linear models are used (see below).

A primary input into regional models is an ecological classification of the study area, including the identification of primary habitat types. Then specific succession classes must be identified, since they emerge in every habitat following most common types of initial shocks (past investations, forest fires, etc.).

At the ecosystem level, forecasting for each forest type is carried out using an ecological model describing the integrated dynamics of the dominating species. The model should be sufficiently universal that it is possible to describe long-term ecosystem behaviour following any set of initial conditions created by exogenic factors under study, for all habitat types.

A principal feature of forest vegetation is that its succession dynamics is rather long-term (10^2–10^3 years) as compared to the observation period accessible to an individual researcher (10^1–10^2 years). The difference in these time scales calls for the employment of an indirect method for study of the development of forest vegetation:

(1) a number of areas with approximately similar ecological conditions but with different stages of vegetation are selected;

(2) an assumption is made that these areas reflect different development stages of one and the same area shifted in time;

(3) based on selected sets of characteristics, these forests are arranged in order, representing their temporal sequence.

Although this indirect method is the only method available and is easy to use, extrapolations forward in time are uncertain. For a vast territory with contrasting ecological conditions subjected to various effects, the number of observed and theoretically possible genetic lines of development is extremely high. Long-term observation of succession dynamics at "typical" sites is impossible. Thus, we believe that the only method of forecasting is to construct a dynamic, multi-species, age-distributed quantitative model, correlated with the ecological conditions of the territory insofar as far as data permit. The model is considered not only as a means of making projections, but also as an instrument for ecological research.

One such model which has been verified by field data [2,14] is described below.

AN EXAMPLE OF A ECOSYSTEM MODEL

We propose a dynamic-demographic approach [7], which implies that the form of the frequency distribution of tree ages is the result of birth and death processes. In the following, the analysis is made in terms of competition properties, seed production intensities, mortality probabilities for each age, seed germination probabilities and so on. Several demographic models of population dynamics have been described in a number of papers. Some of the models are linear [3,5], i.e. the tree mortality probabilities are density-independent; evidently such models are adequate only for short periods of time. The proposed non-linear models (e.g. [4]) require large volumes of ecological data and they are still not completely realistic in the ways that they describe ecological mechanisms.

We have attempted to formulate a relatively simple model, which requires only data obtained during conventional-type forest surveys. A feature of our approach is that some of the hard-to-measure ecological parameters are estimated by adjusting theoretical age distributions (obtained from a model) to empirical ones. Then these parameters are used in model projections.

Below we shall describe some particular features of age distributions, a question that promoted the construction of this model. A typical age distribution form for forest vegetation with a relatively high density of mature individuals is presented qualitatively in Figure 1. This form is typical of forest stands of dark coniferous [10,16,20], beech [8], and oak [8]. Similar distributions have been observed in various stages of a deciduous — dark coniferous succession in the Central Ob region. The non-linearity and non-monotonicity curve shows that the situation is non-stationary, i.e. the system is far from reaching a climax. The type of curve presented in Figure 1 is associated with a situation in which a major part of the forest was destroyed (e.g. by clear cutting, forest fire) T years ago. The "package" of senior ages on the right-hand side of Figure 1 represents individuals that occupied the forest during the first decades after the shock. These species suppresed further regeneration, which explains qualitatively the emergence of the "valley" in the medium-age group. A quantitative description of this "valley" requires the employment of an essentially non-linear model.

Of great interest is the task of estimating the conditions under which the "package" of mature individuals occurs and of tracing the dynamics, subject to the ecologically interpreted model parameters.

Another task is estimation of the success of regeneration. Since juvenile dynamics depends primarily on the state of the parent stand, a forecast of regeneration can be accomplished only within the framework of a general forecast of the dynamics for individuals of all age groups.

Finally, there is a range of problems concerning a change of species in the course of succession dynamics. The description of such changes also requires age-distributed models — in this case, though, for each species. As a first attempt of this kind, we shall use our model to describe a two-species succession.
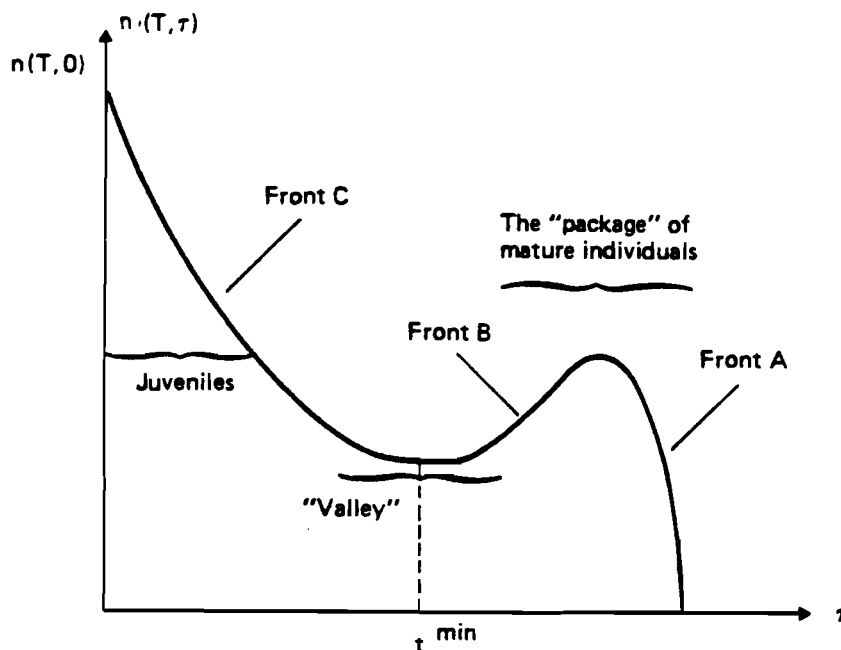
Figure 1: A qualitative picture of the frequency distribution of tree ages observed in a species following destruction of the forest stand T years ago. $n(T,\tau)$ - the number of τ-aged individuals at the Tth moment, $n(T,o)$ - the intensity of invasion.

When formulating the model, we adhered to the principle of "the least number of descriptive variables", i.e. we made use of a very limited set of variables, sufficient for adequate description of the empirical data. Additional input variables would be appropriate only in cases where the effects cannot be explained by the "standard" set of variables. The hasty use of an "excessive" set of variables inevitably leads to rather speculative model projections, owing to the usual lack of field data.

The simplest possible set of variables for an age-distribution model includes values $n_i(t,\tau)$, where i is the species number, and n is the quantity of individuals at age τ at time t. We consider the age dependencies of tree heights and diameters to be fixed, i.e. they do not depend on their current numbers $n_i(t,\tau)$. the introduction of more complex growth processes would at least double the number of variables and make the model

more complicated. Introduction of distribution by dimensions d in every given age, i.e. operating with $n_i(t,\tau,d)$ values would make it even more complicated.

Assume that lifetimes of two coexisting species are P and Q. Then we divide the life cycle of individuals into yearly intervals. The numbers of individuals for each such interval is $X_i (i = 1, \ldots, P)$ for the first species and $Y_k (k = 1, \ldots, Q)$ for the second one; a unit area of one hectare is considered. For simplicity the variable t is omitted. Since we are to describe the whole span of the age curve, the first classes $i = k = 1$ give the respective quantities of seeds X_1 and Y_1. Let us introduce the following notations:

α_i and β_k represent fertilities, i.e. the average number of seeds produced annually by the first species at age i and the second one at age k;

a_i and b_k stand for survivability coefficients from age i to age $i + 1$ (and, respectively, from k to $k + 1$);

Obviously a_i, $b_k \leq 1$ and $1 - a_i$, $1 - b_k$ are annual death rate coefficients;

f_1 and f_2 are equivalent to the annual seed immigration rates of the first and the second species respectively, per unit hectare of the study area.

Let us divide the ecological factors influencing the life cycle into two groups — density-independent and density-dependent ones and let us present fertilities and survivabilities in the form of a multiplication of density-independent and density-dependent factors:

$$\alpha_i = \xi_i \alpha_{oi}(X,Y) \; ; \; \beta_k = \eta_k \cdot \beta_{ok}(X,Y) \; ;$$
$$a_i = c_i \cdot a_{oi}(X,Y) \; ; \; b_k = e_k \cdot b_{ok}(X,Y) \tag{1}$$

In keeping with the view that a restricted set of model variables should be used, all factors of the first type are supposed to be represented by the parameters of the model.

The dependence of the introduced values α_{oi}, β_{ok}, a_{oi}, b_{ok} on the densities X, Y is to be found with the help of particular models describing competition and regeneration of the species under consideration. We have taken up the method proposed in [15] as a competition model, which consists of the following. It is assumed that sunlight is the principal density-dependent factor inhibiting species growth in ecosystems; the crown shape of an individual tree is modelled in the form of a horizontal or vertical screen, partially absorbing light; the average amount of light falling on an individual tree of a given size is computed. Let us denote the amount of light for an individual tree at ages i and k as:

$$R_{1i} \, , R_{2k} \qquad (2)$$

Values (2) depend in general on all the variables of the system, i.e. on X_i, Y_k. In our model, we have chosen the simplest way of representing individual trees — by horizontal screens having area S_m at height h_m for age m. In this case according to [7], the values (2) are computed by the formulas:

$$R_{1i} = R_0 S_i \; e \; -\rho_1(\frac{1}{2}S_i X_i + \sum_{j=i+1}^{p} S_j X_j) - \rho_2 \sum_{j=q_i}^{Q} V_j Y_j \quad ;$$

$$(3)$$

$$R_{2k} = R_0 V_k e \; -\rho_1 \sum_{j=r_k}^{p} S_j X_j - \rho_2(\frac{1}{2}V_k Y_k + \sum_{j=k+1}^{Q} V_j Y_j) \quad ;$$

Here R_0 is the intensity of the initial light flux;

S_i, V_k are surface areas of individuals (in our particular model — the area of horizontal screens);

ρ_1, ρ_2 — light absorption coefficients for screens of the first and the second type;

q_i — the minimal age j when screen j of the second type becomes higher than screen i of the first type;

r_k — the minimal age j, when screen j of the first type becomes higher than screen k of the second type.

Through indices q_i and r_k, our model captures the simple fact that each screen is in the shadow of higher ones. It should be noted that a similar idealization is used in a group of closely related models of forest dynamics that originate from [3,22]. (A model in which individuals are vertical screens would be more realistic but would require much more complex formulas for R_{1i}, R_{2k}.)

For practical application, our model must be modified from an exact one for the screen populations into a semi-empirical model for real populations. Let us assume that S, V are effective areas of individuals, and that they are proportional to the squares of heights $S \sim h^2$, $V \sim g^2$ from dimensional considerations. Further, instead of absorption coefficients P_1, P_2, we introduce empirical coefficients

$$\vartheta_1, \vartheta_2 \tag{4}$$

which are equal to the "effective" absorption coefficients, i.e. ones taking into account the volume and shape of tree crowns, the density and orientation of their phytoelements, i.e. all their deviations from ideally homogeneous flat screens, and also including proportionality coefficients between S and h^2 and between V and g^2.

The model of regeneration (ontogenesis) should be constructed so as to describe the dependence of fertilities and survivabilities on the resource quantities (2) available for the individuals, i.e. the functions should be of the form

$$\alpha_{oi}(R_{1i}) ; \quad \beta_{ok}(R_{2k}) ; \quad a_{oi}(R_{1i}) ; \quad b_{ok}(R_{2k}) \tag{5}$$

The interpretation of this case is a difficult biological-mathematical task, which does not yet have an acceptable solution. Therefore, we used the simplest and biologically adequate assumptions to estimate functions (5). It was assumed that in every age group these functions are equal to the value of the resources available per unit area of an individual's surface

$$\alpha_{oi} = (R_{1i}/R_o h_i^2)^{\delta_1} ; \quad \beta_{ok} = (R_{2k}/R_o g_k^2)^{\delta_2} ;$$

$$(6)$$

$$a_{oi} = (R_{1i} / R_o h_i^2)^{\delta_1} ; \quad b_{ok} = (R_{2k} / R_o g_k^2)^{\delta_2} ;$$

A power-law dependency on parameters δ_1, δ_2 is used because of our desire to obtain from these parameters the simplest form of density-dependent survivabilities and fertilities

$$\alpha_{oi} = a_{oi} = e^{-\gamma_{11}(\frac{1}{2}S_i X_i + \sum_{j=i+1}^{P} S_j X_j) - \gamma_{12} \sum_{j=q_i} V_j Y_j} ;$$

$$(7)$$

$$\beta_{ok} = b_{ok} = e^{-\gamma_{21} \sum_{j=\zeta_k}^{P} S_j X_j - \gamma_{22}(\frac{1}{2}V_k Y_k + \sum_{j=k+1}^{Q} V_j Y_j)} ,$$

where

$$\gamma_{11} = \vartheta_1 \delta_1 ; \quad \gamma_{12} = \vartheta_2 \delta_1 ; \quad \gamma_{21} = \vartheta_1 \delta_2 ; \quad \gamma_{22} = \vartheta_2 \delta_2$$

are coefficients of intraspecies (γ_{11}, γ_{22}) and interspecies (γ_{12}, γ_{21}) competition, that take into account both the different absorption capacities (coefficients ϑ_j), and different shade tolerance capacities (coefficients δ_i).

The required model, which is a system of dynamic equations, is constructed by the usual balance method. Let the numbers of individuals at time t be equal to $X_i(t)$, $Y_k(t)$; then at time $t + 1$ we have

$$X_1(t+1) = a_o \sum_{j=L}^{P} \zeta_j \cdot \alpha_{oj}(X,Y)X_j(t) + f_1 ;$$

$$X_{i+1}(t+1) = c_i a_{oi}(X,Y)X_i(t) , \quad i = 1, \ldots, P-1 ;$$

$$Y_1(t+1) = b_o \sum_{j=M}^{Q} \eta_j \beta_{oj}(X,Y)Y_j(t) + f_2 ;$$

$$(9)$$

$$Y_{k+1}(t+1) = e_k \cdot b_{ok}(X,Y)Y_k(t) , \quad k = 1, \ldots, Q-1 ,$$

where a_o and b_o are coefficients of seed adaptability and dispersion taken as density-independent; the dependency of fertilities and survivabilities on X, Y is defined by formulas (6) and (7); L, M are the ages when species become fertile.

Competition coefficients γ_{ij} as well as seed immigration intensities of dark coniferous and deciduous species f_1, f_2 were estimated by adjusting the theoretical by the empirical age-distribution curves.

As a measure σ for finding f_i and γ_{ik}, we took the total (by species and ages) RMS relative deviation of model distributions from the empirical ones per annum

$$\sigma = \sqrt{\frac{\sum_{\tau=1}^{T}\left[\frac{x(T,\tau)-n_1(T,\tau)}{n_1(T,\tau)}\right]^2 + \sum_{\tau=1}^{T}\left[\frac{y(T,\tau)-n_2(T,\tau)}{n_2(T,\tau)}\right]^2}{2T}} \tag{10}$$

where T is the age of succession, and $x(T,\tau)$, $y(T,\tau)$ and $n_1(T,\tau)$, $n_2(T,\tau)$ are theoretical and empirical age distributions of dark conferous and deciduous species, respectively. Optimal values of f_i and γ_{ik}, f_i^{opt} and γ_{ik}^{opt} that yield the minimum for σ were obtained by a variant of the gradient method [18].
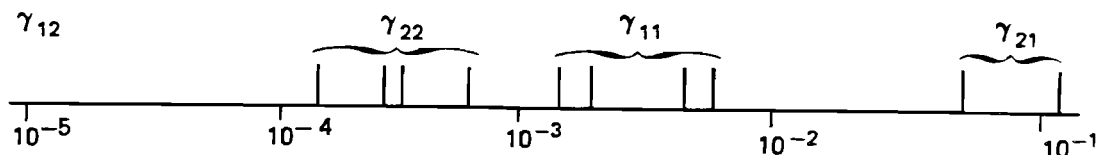
Values of the other parameters were taken from the literature (fertility curves) or estimated during preliminary computations (density-independent mortality curves).

The resulting optimal values of the parameters (in the sense of minimal σ [18]) are presented in Table 1. These results are discussed below.

1. The constants of inter- and intraspecies competition γ_{ik} reveal a grouping for each type of interaction (according to the rows of the table). The clustering is shown in another way on a numerical axis using a logarithmic scale.

---

*The γ_{12} constant turned out to be so small that the gradient method yielded $\gamma_{12} = 0$. Thus, the accuracy of field data proved to be insufficient to determine this constant; beginning with $\gamma_{12} = 10^{-5}$, the value σ (10) ceases to respond to changes of γ_{12}; hence an upper limit is presented in the table.

**Constant γ_{21} here is higher than its real value, since there are no juveniles in the deciduous stands on the test sites, owing to competitive suppression by the dark conifers, as well as by the development of a moss cover. Since the model oes not contain a variable that describes these dynamics, the constant γ_{21} turned out to be too high.

$$\gamma_{12} \qquad \gamma_{22} \qquad \gamma_{11} \qquad \gamma_{21}$$

$$10^{-5} \qquad 10^{-4} \qquad 10^{-3} \qquad 10^{-2} \qquad 10^{-1}$$

The groups are distributed as might be expected from a consideration of species distributions and shade-tolerances. This grouping seems to confirm that all four test sites, which have been used to adjust the model, belong to the same succession line, i.e. ecological conditions at these sites are similar.

The grouping of uniform γ_{ik} implies that mean values of parameters γ_{ik} should give suitable projections of behaviour at each test site. Actually, we have one of the possible verification variants: assuming that the sites belong to the same succession line, we find that the γ_{ik} grouping testifies to the adequacy of the succession model used; if the model is adequate, then the sites should belong to the same succesion line.

2. The smallness of the values of parameter γ_{12} — the competitive influence of the deciduous species on the dark coniferous one — proves that the latter is actually "autonomous", and that the former has no effect on it. On the contrary, the deciduous species is "the follower" here, i.e. the influence of the dark coniferous species on the shorter deciduous trees is much stronger than the self-induced effects of the latter. The "package" of deciduous individuals, having "escaped" from the influence of the dark coniferous species is affected only by intraspecies competition.

3. We have examined variations of values γ_{ik} for each area in order to clarify the model's sensitivity to changes of these central parameters. For this purpose, σ isolines were found corresponding to a 20% deviation from σ^{min}; taking into account the relatively low accuracy of the quantitative description we believe that a 20%

Table 1: Results of model adjustment to empirical age-distributions

Succession age T years		100	120	160	180
Constants of competitive interactions	γ_{11} (dark coniferous-dark coniferous)	0	0	0	0
	γ_{12} (deciduous-dark coniferous)*	$<10^{-5}$	$<10^{-5}$	$<10^{-5}$	10^{-5}
	γ_{21} (dark coniferous-deciduous)**	0.1	0.13	0.08	0.07
	γ_{22} (deciduous-deciduous)	0.00036	0.00069	0.00041	0.00021
Intensity of seed immigration number per hectare	f_1 (dark coniferous)	1645	1550	1550	2000
	f_2 (deciduous)	100000	75000	100000	1000000
Juvenile survivability of dark coniferous species	$\prod\limits_{k=1}^{N} C_k$ $K=1$ (see Eq. 1)	0.069	0.059	0.047	0.025
The age since $C_t = 1$	N years	20	17	50	46
RMS deviation values	σ^{min}	0.53	0.56	0.51	0.53

value (but not lower) is reasonable. We assume that within the domain

$$\omega \leq 1.2 \, \sigma^{min} \tag{11}$$

any value of γ_{ik} gives a reasonable system dynamics projection. For brevity, we consider domains ω_1, ω_2, ω_3, ω_4 corresponding to areas with $T = 100$, 120, 160, 180 years. Out of all possible two-dimensional projections, we shall cite a particular one, namely $(\gamma_{11}, \gamma_{22})$; see Figure 2. (Note that parameter γ_{11} has a stronger effect than the others on the form of the theoretical curve $x(T, \tau)$ and the degree of adjustment, i.e. the value). Greater extension of all domains ω_1 along coordinates γ_{22} compared to γ_{11} obviously corresponds to greater control of the dark coniferous as compared to the deciduous species, since the system responds by strong changes of age distributions to the variation of γ_{11} and by weak ones — to the variation of γ_{22}. for $T = 100$, the domain is extended along γ_{22} much less than along the others — this is obviously due to a relatively underdeveloped dark coniferous population. So, changes of the form from ω_1 to ω_2 reflect the rapidity with which the dark coniferous species take control of the succession dynamics.

APPLICATION OF THE MODEL

The model can be used for quantitative projections of deciduous — dark coniferous succession under various scenarios:

1. having determined certain initial distributions of $x(o, \tau)$, $y(o, \tau)$, one can describe the effect of a partial burning of the forest with subsequent regeneration;

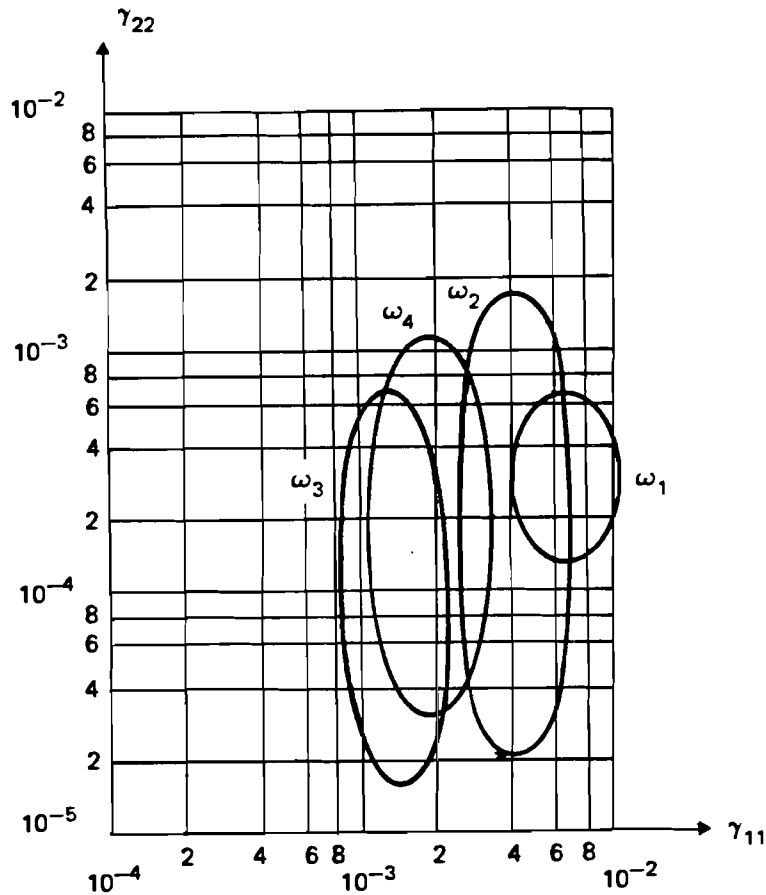2. by reducing the population numbers in some age groups at a given time, one can simulate selective cutting;

Figure 2:   Isolines of σ which correspond to a 20% deviation from σ^{min}; ω_1, ω_2, ω_3, ω_4 correspond to the sites with succession ages $T = 100, 120, 160, 180$, respectively.

3.   by slightly modifying the system parameters, one can estimate the forest's response to weak "background" impacts and thus use the predictions for the purpose of vegetation monitoring [12].

Simulation of effects caused by climate change was carried out by introducing an external factor, which inhibited or stimulated the increase of tree height and diameter, according to a time-exponential law. We have considered in greater detail the course of succession with the parameters given in Table 2 and with

$$h_t = h_{to}e^{\lambda t} \; ; \; g_k = g_{ko}e^{\mu t} \tag{12}$$

where rates of increment changes λ, μ may be of either sign. Of all possible characteristics of succession, we have studied two features of primary interest, viz., the number of mature individuals, $N_{1,2}$ and their biomasses $M_{1,2}$. The impact intensities (the values of λ, μ) are supposed to be weak, so alterations of N and M may be found in the form

$$N_1 = N_{01}(1 + a_1\lambda + a_2\mu) \quad ; \quad N_2 = N_{02}(1 + a_3\lambda + a_4\mu) \quad ;$$

(13)

$$M_1 = M_{01}(1 + a_5\lambda + a_6\mu) \quad ; \quad M_2 = M_{02}(1 + a_7\lambda + a_{\langle}\mu) \quad ,$$

where a_i are respective logarithmic derivatives taken in the unperturbed state $\lambda = \mu = 0$. Note that all values in (13), except for λ and μ depend on the age of succession T.

The biomass of each species was found by the formula

$$M = \sum_{i=i_0}^{T} \Psi_i H_i \frac{\pi}{4} D_i^2 N_i \quad ,$$

(14)

where i_0 is an initial time, viz., the time when the individual trees became mature. (During the adjustment of the model, it was established that the best coincidence of N_1^{theor} and N_2^{exp} is achieved when $i_0 = t^{min} - 15$ (Figure 1) for the deciduous species.)

i_0 was set equal to t^{min} on the curve $y_j(t)$; see Figure 1;

Ψ_i are the corrective coefficients for calculation of stem volume;

$H_i = h_i$, g_i are tree top heights for the two species, determined from (12);

$D_i = d_{1i}$, d_{2i} are the stem diameters of the two species defined by formulas, similar to (12)

$$d_{1i}(t) = d_{io1}e^{\lambda t} \quad , \quad d_{2i}(t) = d_{io2}e^{\mu t}$$

(15)

where d_{io1}, d_{io2} are unperturbed curves of diameter growth, obtained from test site data. So it is assumed that the growth process of each species conserves tree shape. The partial derivatives a_i in (13) were estimated at the point λ, $\mu = 10^{-3}$.

Table 2: Parameter values of a deciduous — dark coniferous succession model for one of the test sites

		Age of succession T	120
Constants of competitive interaction	γ_{11}	(dark coniferous–dark coniferous)	.004
	γ_{12}	(deciduous–dark coniferous)	10^{-5}
	γ_{21}	(dark coniferous–deciduous)	.13
	γ_{22}	(deciduous–deciduous)	.0007
Intensity of seed immigration number per hectare per annum	f_1	(dark coniferous)	1550
	f_2	(deciduous)	75000
Parameters of the curve representing density-independent juvenile survivability of dark-coniferous species	N	the age since $C_t = 1$ (see Eq. 1)	17
	K_1		.7
	K_2		.0176
Initial fertile age	L	(dark coniferous)	80
	M	(deciduous)	20
Seeds' survivability coefficient	a_0	(dark coniferous)	.005
	b_0	(deciduous)	.001
Maximal fertility coefficient	ξ_p	(dark coniferous	200
	N_q	(deciduous)	10^6

The results are presented for the test site with constants from Table 2. Values a_t were found for $100 \leq T \leq 160$.

$$N_1 = N_{01}(1 - 170\lambda - .1\mu) \quad ;$$

$$N_2 = N_{02}(1 - 14\lambda - 29\mu) \quad ;$$

$$\text{(16)}$$

$$M_1 = M_{02}(1 + 200\lambda + .2\mu) \quad ;$$

$$M_2 = M_{02}(1 + 8\lambda + 260\mu) \quad ;$$

Values a_1, a_2, a_3, a_6, a_7 have proved to be almost independent of succesion age T; values a_5, a_8 show a weak dependence on T and are given in (16) for $T = 120$. Due to the weak influence of the deciduous species on the dark-coniferous one, a_2 and a_6 are very small.

Note the influence of growth rate changes of each species on the numbers and the biomasses:

1)   when growth is suppressed (λ, $\mu < 0$), the population numbers increase while their biomasses decrease;

2)   when growth is stimulated, the effect is reversed; here we have a purely ecological (or competitional) compensation effect, since in the absence of competition, the biomass change would have been much greater.

Let us give an example, a change in temperature T^{*}. As is known [17], a 1^{*} increase in T^{*} (all other parameters remaining in the optimum zone) leads to a 10% biomass increase, which corresponds to a 3% change in tree heights and diameters. Let us assume that the change of 1^{*} in T^{*} takes place during 30 years. Then the annual increase in linear dimensions is equal to

$$\lambda = \mu = .03/30 = 10^{-3}$$

(such values give a 10% change in tree heights and diameters over 100 years).

For these λ, μ values and for the study test site, some results are presented in Figure 3 and 4. In particular, for a succession which began in 1980, the change in population numbers in the dark-coniferous species would be -17%, while by the year 2100 the increase in biomass would be +20%.
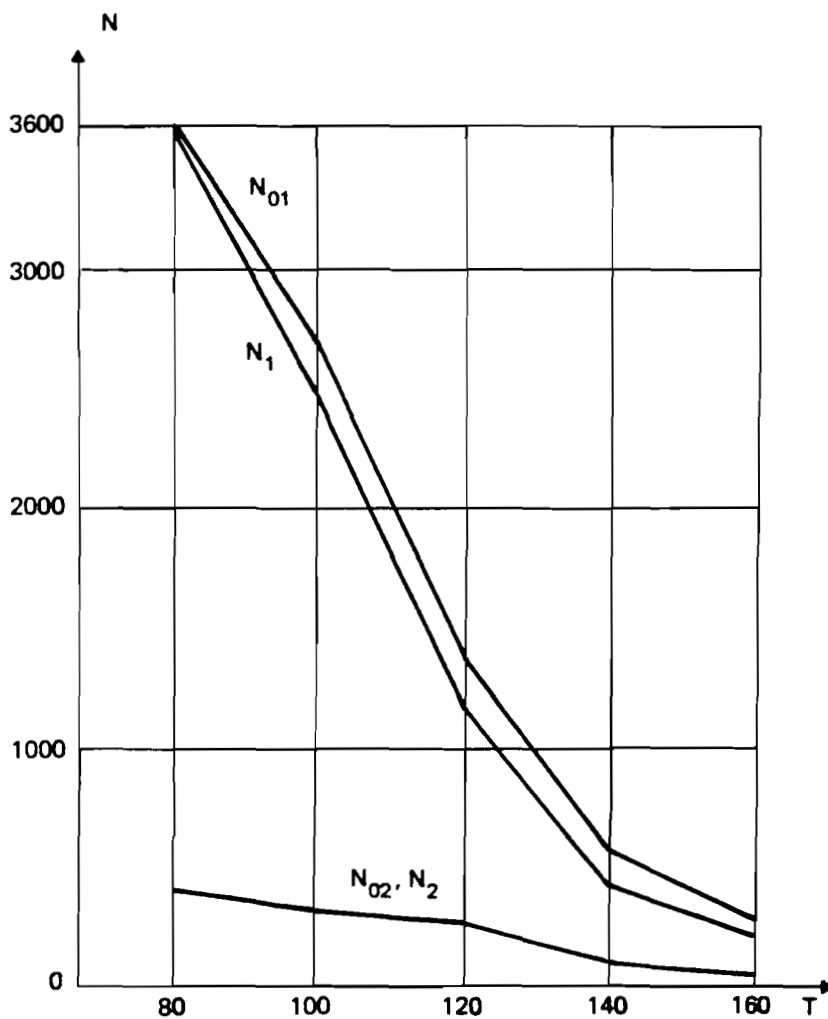
Figure 3:   Dependence of the population numbers of mature individuals on succession age T. N_{o1}, N_{o2} are the unperturbed ($\lambda = \mu = 0$) numbers of the dark-coniferous and the deciduous species, while N_1, N_2 are those perturbed, with $\lambda = \mu = 10^{-3}$.

For factors having non-equal influences on the two species, the impacts can be examined in a similar way. (For example, a reduction of light flux due to an increased atmospheric aerosol loading would exert a heavier impact on the light-requiring deciduous species than on the coniferous one.)

AN EXAMPLE OF A REGIONAL-SCALE FORECAST

The mathematical technique for prognosis is as follows. First the region being studied is subdivided into habitats of types $j = 1, \ldots, R$, each having its own intrinsic successional dynamics following exogenous disturbances. In its turn, each succession line is subdivided into discrete states (or stages) $n = 1, \ldots, Q$ including all the states that have appeared due to exogenous disturbances and endogenous dynamics. Let us introduce the quantities p_{jn}, which represent fractions of the territory, related to habitats with ecosystems at state n. We shall limit our discussion to the case of ecosystems that do not interact, i.e. they have their own endogenous dynamics and do not influence their neighbours across the boundary. Then the dynamics of fractional areas are described by a linear Markovian system [22]

$$p_{jn}(t+1) = p_{jn}(t) + \sum_{s}^{Q} a_{jns}(f)p_{js}(t) \quad , \tag{17}$$

where $a_{jns}(f)$ are the transition probabilities from succession stage n into stage s; these values describe both endogenous factors and the replacement of stages due to exogenous disturbances; f represents climate parameters and the physico-chemical state of the atmosphere; t is time.

To simplify our task, we shall not deal with population dynamics, but will describe the state of the ecosystem by only one variable for each species i, i.e. by its biomass:

$$m_{ij}(n+1) = g_{ij}[m(n), q, f] \quad , \tag{18}$$

where i is the species number, j the type of habitat, n the stage of successions q are parameters, and f is as defined earlier. For the sake of simplicity it is assumed that all successional stages last the same length of time, viz., the time step in (17).

The essence of the proposed forecast scheme is the simultaneous use of models (17) and (18); the latter is based on the several exogenous effect-mechanisms, which could be "soft" or "hard". The former include factors that weakly change the parameters of the vegetation environment. All the explicit background factors along with some implicit ones (e.g. bogging) are
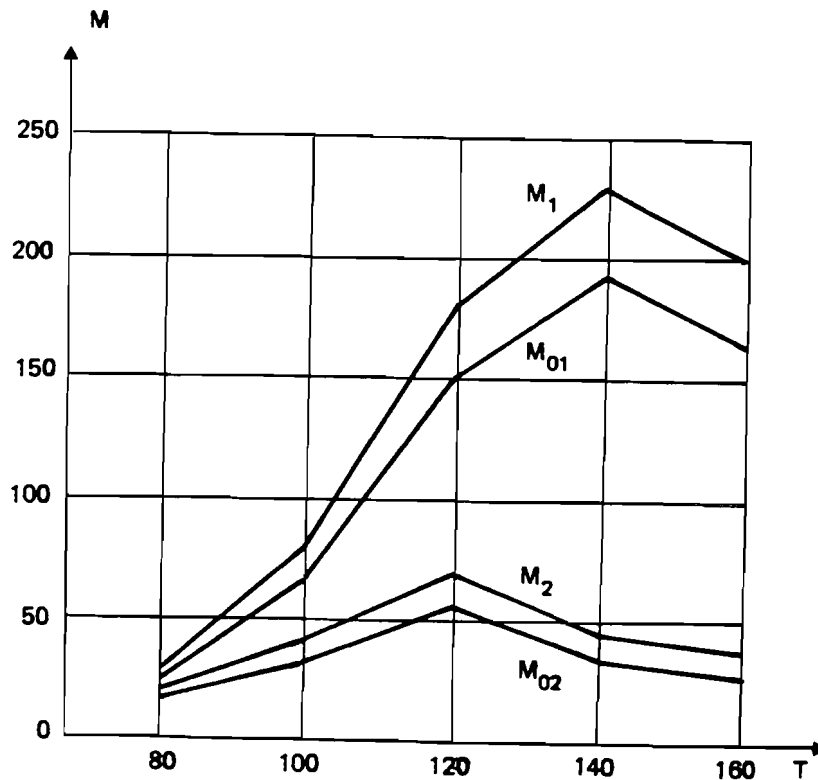
M

Figure 4: Dependence of mature individuals' biomasses on the succession age T. M_{01}, M_{02} are the unperturbed $(\lambda = \mu = 0)$ biomasses of the dark-coniferous and deciduous species, and M_1, M_2 are those with a $\lambda = \mu = 10^{-3}$ perturbation.

in this group. The second type comprises factors that change the affected ecosystem rather rapidly into another state — these factors include forest fires, strong windfalls and pest infestations; such effects do not change the "state" of the Markovian system (17). For this reason, background factors (weak by definition) are not included in transition probabilities a describing endogenous changes, but they are included in probabilities of intermittent transitions that occur under the influence of "hard" factors. Changes of productivity, fertility and survivability, arising from the influence of "soft" background factors are taken into account in the model (18). The effect of hard factors is not described by this model.

Let us have a habitat of a given type, occupied by a single dominant species; therefore we can drop the index k for p, a values in (17) as well as i and k indices for m in (18). Let the territory be in a state of equilibrium as a whole, i.e. the fractions of areas P_n covered by each of the successional stages are constant. Suppose there is a weak change in the value of one exogenous parameter, $\Delta f / f \leq 1$. This effect, which is soft at the ecosystem level, would change the mean values of the biomasses at each successional stage

$$m(n, f + \Delta f) = m(n, f)[1 + \mu(n, f)\Delta f]$$

At the regional scale, forest fire burn-out probabilities would change slightly for each succession stage

$$a_{ns}(f + \Delta f) = a_{ns}(f)[1 + a_n(f)\Delta f]$$

along with equilibrium fractions of areas

$$P_n(f + \Delta f) = P_n(f)[1 + \pi_n(f)\Delta f]$$

The parameters μ, a, π are coefficients of susceptibility to factor f.

The total biomass of the species under consideration per unit regional area is

$$M = \sum_n m(n, f)[1 + \mu(n, f)\Delta f]P_n(f)[1 + \pi_n(f)\Delta f] \cong$$

(19)

$$\sum_n m(n, f)P_n(f) + \Delta f \sum_n m(n, f)P_n(f)[\mu(n, f) + \pi_n(f)]$$

Let us try to assess the values $\mu(n, f)$, $\pi_n(f)$. Suppose the factor f is temperature, and $\Delta f = 1°$. For boreal forests, values of $\mu(n, f)$, are in the order of 0.05–0.1 1/deg [11]. Assessment of $\pi_n(f)$ is more difficult. For taiga forests, the burn-out probability ($k \to 1$) transition is approximately equal to 10^{-2} 1/per annum [11]. When the climate warms, this value changes (mainly due to the variation of frequency of drought years). For the European part of the USSR during the next several decades, the projected change of this value due to greenhouse warming will be within the range of from 0.3 to 0.4 1/per annum. Assuming that the burnout probability

increases in the same proportion, it follows that $\alpha_{n1} \cong 0.3$, and $\alpha_{n1}(f + \Delta f) = 0.01(1 + 0.3\Delta f)$. By taking reasonable steady state values $P_n(f)$, it is easy to show that the change of $P_n(f)$ has the same order of magnitude as $\alpha_n(f)$, the calculation being carried out in accordance with (17), i.e. that $\pi_n(f) \cong -0.3$. So values of the summands within every pair of brackets in (19) differ slightly but have opposite signs, i.e. the biomass increase effect at the ecosystem level would be compensated by its decrease at the regional level. The authors believe that this preliminary assessment indicates that a more detailed study should be undertaken.

IMPLICATIONS OR ECOSYSTEM MONITORING

There is growing recognition of the need to establish monitoring systems to provide early indications of ecosystem change; see, for example, [21].

It is our belief that specialized information services should be established for this purpose at the regional level.

The technological basis for the information services should be provided by remote sensing and thematic interpretation of imagery, one of the first tasks being to undertake a regional ecological survey. This would include:

- data on the fractions of land surfaces occupied by each of the primary vegetation types (forests, meadows, bogs) at circa $1:10^6$ scale imagery;

- descriptions of the ecosystems within each vegetation type (a listing of dominants, the number of individuals) by means of circa $1:10^5$ scale imagery and supporting information from ground-truth sites;

- information on current exogenous stresses (climate anomalies, recent forest fires, pst outbreaks, etc.).

Prediction of future regional ecosystems states would be based on the models described in [9], [18] and [17], values of the input parameters being obtained from the ecological survey data described above. At regular intervals, the survey should be repeated to update the predictions, and to

obtain a growing file of time-series data.

Summarizing, it is the opinion of the authors that highly aggregated forestry information will not be particularly useful in predicting the ecological impact of an exogenous stress such as a forest fire, climate anomaly or pest outbreak. Instead, it will be necessary to collect detailed information on ecosystem structure (dominant species, age distributions, susceptibility to damage by pests, etc.). This information should be obtained in an integrated way over an entire region.

REFERENCES

1. Antonovsky, M.Ja., Korzukhin, M.D. Mathematical modeling of economic and ecological-economic processes. *Proc. 2nd International Symposium*, Tbilisi, 1981, "Integrated Global Monitoring of Environmental Pollution", Leningrad, Gidromet, 1983.

2. Antonovsky, M.Ja., Korzukhin, M.D. and Ter-Mikaelyan, M.T. Mathematical modeling of antronogenic changes in forest ecosystem. *Proc. 1st Soviet-French Symposium*, Moscow 1984, Gidrom.

3. Botkin, D.B., Janak, J.F. and Wallis, J.R. Some ecological consequences of a computer model of forest growth. *J. Ecol.*, 60(1972), 849–872.

4. Cherkashin, A.K. Dynamics model of a taiga biogeocoenosis. In: Optimal Management of Nature-Economics Systems. Nauka Publishers, Moscow, 1981 (in Russian).

5. Cherkashin, A.K. and Kuznetsova, E.I. A study of trees dynamics for the empirical substantiation of mathematical methods used in forest development forecasting. In: Temporal Changes of Natural Phenomena. Nauka Publishers, Novosibirsk, 1979, (in Russian) 46–56.

6. Delcourt, H.R., Delcourt, P.A. and Webb, T. Dynamic plant ecology: the spectrum of vegetational change in space and time. *Quarternary Science Reviews*, 1(1983)153–175.

7. Demography and evolution in plant populations. *Botanical Monograph*, 15(1980).

8. Dolukhanov, A.G. On some regularities of the development and change of primary formations of the Caucasus forest vegetation. In: *Proceedings of the Tbilisi Botanical Institute*, Vol. 19, 1–68, 1958 (in Russian).

9. The Dynamic Theory of Biological Populations. Moscow, Nauka, 1974 (in Russian).

10. Dyrenkov, S.A. Structure and dynamics of spruce forests of central and southern taiga zones in the European North. Author's abstract of the Doctoral thesis, Leningrad, 1976.

11. Furyaev, V.V. and Kireyev, D.M. The Landscape-based Study of Post-fire Dynamics of Forests. Nauka, Novosibirsk, 1979 (in Russian).

12. Izrael, Y.A. The assessment of the state of biosphere and rationale of monitoring. Proceedings of the USSR Academy of Sciences, Vol. 226, No. 4, pp. 955–957, 1976 (in Russian).

13. Izrael, Y.A. Ecology and Control of Environment, 2nd edition, Gidrometioizdat, Moscow, 1984.

14. Korzukhin, M.D., Sedykh, V.N. and Ter-Mikaelyan, M.T. Formulation of a prognostic model of age dynamics, *Lesovedeniye Journal*, forthcoming (in Russian).

15. Korzukhin, M.D. and Ter-Mikaelyan, M.T. Competing for light and dynamics of model individuals independently distributed on the plane. In: *Problems of Ecological Monitoring and Ecosystems Modelling*, Vol. V, Hydrometeoizdat, 184—192, 1982 (in Russian).

16. Krauklis, A.A. and Bessolitzina, E.P. Age succession changes of the taiga biogeocoenoses. In: *The Study of Site of the Taiga Geosystems*, 152—174, Irkutsk, 1980 (in Russian).

17. Larcher, W. Plant Ecology, Mir Publishers, Moscow, 1978 (in Russian).

18. Ortega, J. and Reinboldt V. Interaction Methods of Solving Systems of Non-linear Equations with Many Unknowns. Mir Publishers, Moscow, 1975 (in Russian).

19. Munn, R.E. The Design of Integrated Monitoring Systems to Provide Early Indications of Environmental/Ecological Changes, WP-85-71, IIASA, Laxenburg, Austria.

20. Regulation Factors of Spruce Forest Ecosystems. Nauka, Leningrad, 1982 (in Russian).

21. Shugart, H.H., Grow, T.R. and Hett, J.M. Forest succession models: a rationale and methodology for modeling forest succession over large regions, *Forest Science*, 19(1973)(3)203—212.

22. Shugart, H.H., West, D.C. and Emmanuel, W.R. Pattern and dynamics of forests: an application of simulation models. In: Forest Succession, 1981, pp. 74—94.

23. Shugart, H.H. Forest Dynamics, Springer—Verlag: Berlin, 1984.

24. Spurr, S.H. and Barnes, B.V. Forest Ecology. Lesnaya Promyshlennost Publishers, Moscow, 1984 (in Russian).