

WORKING PAPER

MONITORING LONG-TERM CHANGES IN THE
BOREAL FOREST

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FOREWORD

This paper was presented by Michael Antonovsky at the Second Symposium on Space and Global Change (October 9, 1986; Innsbruck, Austria) sponsored by the International Astronautical Federation. The research reported is part of the continuing happy collaboration between Professor Antonovsky and Professor Shugart of the University of Charlottesville in the United States.

As pointed out in the conclusion, "There is a general convergence of forest models being developed in the USSR and the USA in terms of the philosophy that underlines the modeling approach." However, there are differences in realization so that comparisons as given in the paper represent "a very useful scientific endeavour".

This Working Paper is a contribution to the monitoring research activity being developed within the IIASA Environment Program. The results are also a contribution to the new ICSU Global Change Programme.

R.E. Munn
Leader
Environment Program

MONITORING LONG-TERM CHANGES IN THE BOREAL FOREST

M.Ja. Antonovsky* and H.H. Shugart**

Forest ecosystems contain a complex web of interactions among physical, chemical and biological processes. Because of this interactive complexity, direct changes in a given process can be attenuated or amplified, and the responses elicited from a forest will be manifested on many different time scales.

Tree growth results from the amount of photosynthate produced and the allocation of this photosynthate within the tree. The growth of trees has been modelled using "mechanistic" representations of physiological processes, but these models have rarely been used to predict responses over periods longer than a year.

It is important to note: (1) that the web of interactions is complex and the details of some of the interactions are not well known, and (2) that the response of the whole plant to a stress may be non-linear across the possible range of that stress. In general, the fast processes that operate in forest ecosystems can only be predicted over the longer term with a considerable degree of uncertainty.

There have been several attempts to develop highly detailed "mechanistic" models of natural ecosystems including forests. These models are useful as heuristic tools for integrating studies of different ecological processes, but are much less useful for predicting long-term ecosystem behaviour.

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Environmental change can affect the growth rates of individual trees and thereby have a cumulative effect in changing the amount of living material in the forest system. However, the relation between the rate of individual tree growth and the rate of forest increase (or yield) is more than a simple additive effect. Relatively low levels of stress on trees can produce large changes in the dynamics and composition of forests. Furthermore, the interactions between the populations of trees and insects (and other pests and diseases) are, in many cases, mediated by climate and thus are of importance in assessing the possible effects of climatic change on forests. For example, the oak-wilt disease in the USSR appears to be dependent on the decreased ability of the trees to resist leaf-eating insects during drought (Israel et al. 1983).

The prediction of yield from growth has been an important topic in modern forestry (Fries 1974). Forest yield is a consequence both of the growth of individual trees and of the rates of recruitment and death of trees in the forest stand. For example, Figure 1 illustrates the relation between stand biomass and the age of stands of *Picea glauca* forests (Yarie and Van Cleve 1983). Over the time period indicated by the different ages, the growth increment of the trees was constant (diameter increase = 0.11 cm/year; r^2 of regression = 0.87) but the rate of increase of the total biomass clearly declined as a function of age. In contrast, the rate of biomass change of a single tree, which was enlarging with a constant diameter increment, increased with the size of the tree (because tree biomass is a power function of the diameter). Thus, the change in biomass growth rate shown in Figure 1 was opposite to that of the individual trees that comprised the forest. Effects such as these prevent direct extrapolation of short-term changes in trees to predict the longer term responses of the forest.

The modern theoretical concept for understanding the intermediate time scale response of a forest is to consider the forested landscape to be a mosaic with each element of the mosaic scaled in relation to the dominant canopy tree (ca. 0.1 ha, depending on the size of the trees). This concept was initially developed by Watt (1925, 1947) and has been the topic of a series of papers and books (Raup 1957; Whittaker and Levin 1977; Bormann and Likens 1979 a,b; Shugart 1984). The concept, in brief, is that the dynamic response of the forest occurs at an areal scale of a large canopy tree and on a time scale that relates to the longevity of the tree, as follows.

"Following the death of a large tree and its fall, a canopy gap forms. The area below this gap becomes the site of increased regeneration and survival of trees. Trees grow, the forest builds, the canopy closes, and the gap disappears. Eventually, the now mature forest in the vicinity of the former gap suffers the mortality of a large tree and a new gap is formed and the cycle is repeated (Shugart 1984)."

The dynamics of a forest are the aggregated dynamics of a large number of such individual gaps. When considered at intermediate time scales (ca. 100 years), the pattern of dynamics of a forest can be seen as a cycle of recruitment, death and growth processes; environmental change alters the pattern within the cycle (Figure 2). The regeneration phase of the forest cycle and the exact timing of the death of a canopy tree that produces an opportunity for regeneration are highly stochastic processes. This is particularly the case in the regeneration phase when the mortality

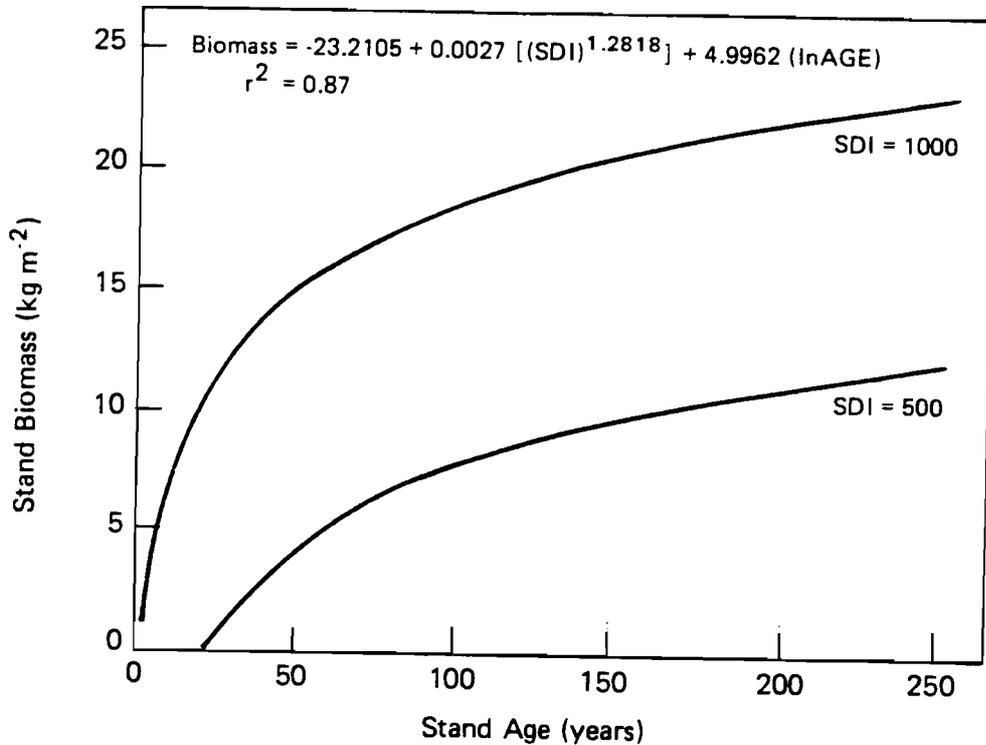


Figure 1: The relationship of above-ground stand biomass to stand age for white spruce (*Picea glauca*) from the Interior of Alaska (from Yarie and Van Cleve, 1983). A fully stocked stand has a site density index (SDI) of 1000; a stand with one half this density of trees has a SDI = 500.

of small trees is very high. It is in this stochastic part of the cycle that climatic change and variability can have the largest influence in producing change in the forest.

Change in the rate of soil development could also greatly delay the response of a forest to a climatic change. The soil at a given location derives its characteristics from the parent material (the geology at the site), the vegetation and the climate. If both the climate and the vegetation at a given location were to change, there might be considerable delays in the development of the soils and, hence, the forests which one would expect ultimately to develop at the site.

Large climatic fluctuations have taken place during the last one hundred years (Wright 1984).

While the use of models offers a means to scale up in both time and space, our present state of knowledge about the processes involved is insufficient to allow this to be done with any real confidence in the results. Consequently, we see a need for the concurrent development of models and

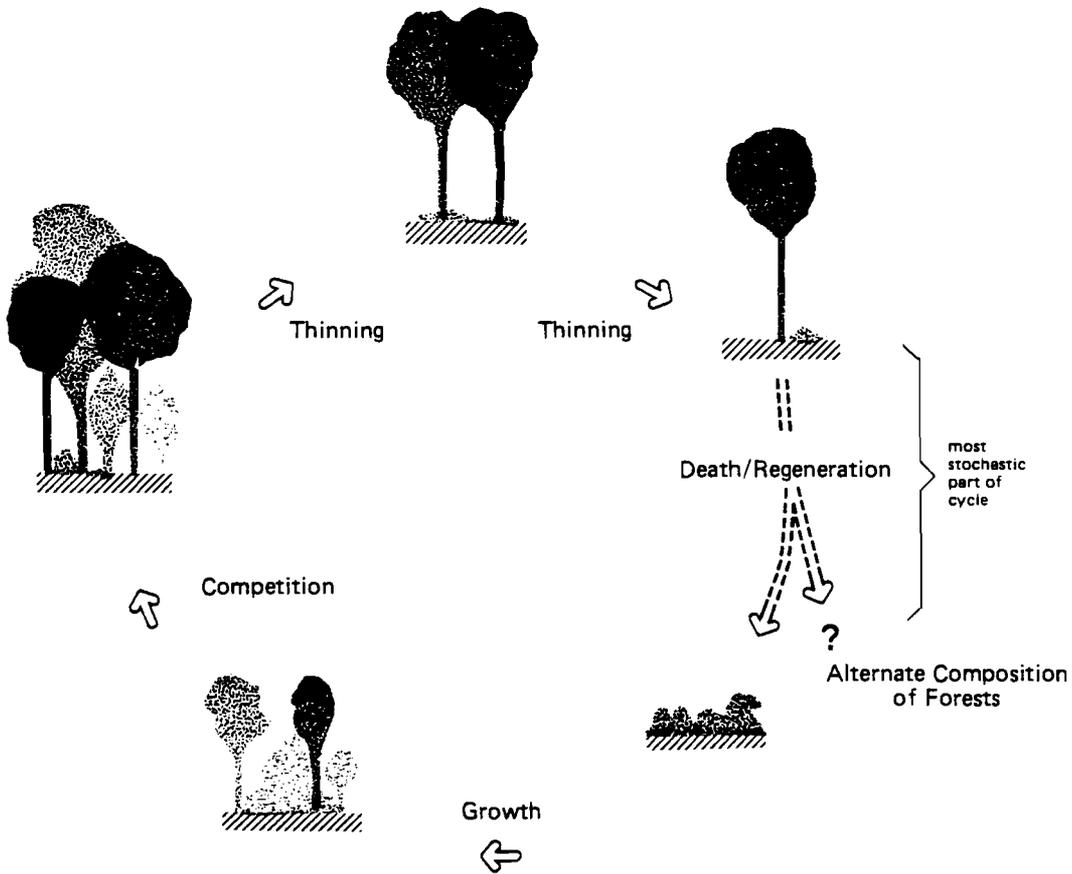


Figure 2: Simulation of the long-term regeneration cycle of forests using the BRIND model (Shugart and Noble, 1981) for the Australian Eucalyptus forest. The determinism in the system is great during the growth, competition and thinning phases but more stochastic in the death and regeneration phases.

empirical studies of the physiological and micrometeorological processes that determine the response to environmental change. Given the paucity of our present knowledge, such empirical studies are needed at each spatial and temporal scale.

Determination of the response of a forest to a climatic change involves evaluation of a complex system with many levels of response. One means of attempting to handle this complexity is by the use of quantitative models of forest dynamics as investigative tools. There are several hundred extant models of forest dynamics that simulate the growth of individual trees to determine the temporal response of a forest. These models seem to be most appropriate to "intermediate time scales" discussed earlier. There have been several reviews of the types and performance of detailed models of forest dynamics (Munro 1974; Shugart and West 1980; Shugart 1984). We will in this paper provide two examples of modeling the dynamics of forests. The first discussion includes a specific example from a hierarchical model of successional dynamics in western Siberia. This example is from Antonovskiy and Korzukhin [1986]. We also will discuss the mapping of global change of forests (Emanuel et al 1985) to climate change as a second example.

EXAMPLE 1. HIEARCHICAL SIMULATION OF VEGETATION DYNAMICS

In conditions of technogenic impacts, the prediction of the state of the biosphere, as a whole, should consider the response of vegetation to changing ecologic parameters, global changes of these parameters following the changes occurring in the state of vegetation.

This section of the paper makes an attempt to further the elaboration of the former, i.e., the internal dynamics of the boreal forest. Thus, we do not deal here with the vegetation→biospheric parameters relationship, but regard this or that scenario of changes in global ecologic (climatic) parameters as preset.

To assess the response of vegetation to changes in ecologic parameters over periods exceeding several years under possibly altered atmospheric conditions, one must construct mathematical models which make use of available information on plant physiology and ecology, as well as on the organisation and structure of vegetative cover. Due to the complexity of the task involved in the construction of models of boreal forest dynamics, and the relatively short period of time elapsed since the beginning of its solution, the simulation of these forests is practically at its starting point. For instance, no adaptation elements (adaptational response of individuals to changes in ecological parameters) are incorporated into existing plant dynamics models.

A phytomass (m) dynamics equation for an individual tree such as,

$$\dot{m} = F - R$$

(F – rate of photosynthesis, R – its products spent for various needs) will become methodologically incorrect if directly applied [Budyko, 1984; Kravivin, 1982], to global or zonal levels. We believe that the most important factor to be taken into account when constructing models of forests, is the hierarchical (multilevel) organisation of vegetation [Razumovsky, 1981; Delcourt, H.R., Delcourt, P.A. and Webb, 1983]. The dynamic nature of the forests and, as a rule, the multiple effects of environmental factors often result in unexpected responses to changes in those factors. Let us consider an example based on the following considerations.

1. *Relationship between individual and ecosystem organisation levels.* Let the increased values of a certain factor $\psi \rightarrow \psi + \Delta\psi$ (e.g. CO_2) stimulate the growth of an individual (a tree) and the accumulation of its phytomass m for any value of age t ($\Delta\psi/\psi \ll 1$):

$$m(t, \psi + \Delta\psi) = m(t, \psi)[1 + a(t)\Delta\psi]$$

Then, let us consider a population of N trees of the same age and the change in its total phytomass $M = N \cdot m$

$$M(t, \psi + \Delta\psi) = M(t, \psi)[1 + b(t)\Delta\psi]$$

As a rule, this change will be less than changes in individual phytomasses m , that is

$$a(t) > b(t) \quad \text{will be true.}$$

Such damping effect is accounted for by ecological interaction: stimulation of an individual's growth results in greater competition and increased mortality, i.e. in a decreased number of individuals in comparison with that observed prior to the alteration of factor ψ . Therefore, as ψ increases, M grows more slowly than m . This result has been obtained in a series of simulation model experiments using models for seven different ecosystems under a condition of increased growth of individual trees (Shugart 1984).

2. *Relationship between various impacts of a given factor at the individual level.* Let us refer to a well-known example dealing with photosynthesis: the increased leaf's exposure to light results in its heating, increased evaporation and, in case of a lack of water in tissues – in the narrowing of stomata and, in the long run, in a smaller buildup of productivity than could be expected in the case of increased exposure to light and water excess in tissues.

3. *Relationship of various impacts of the given factor at the landscape (regional) level.* Over territories with excessive moisture, a temperature increase in boreal forests favours the decrease of swamp areas and the extension of forest covered area. At the same time this condition creates fire hazards which reduces the average forest age. So, despite the extension of forest covered area, the phytomass of boreal vegetation can either increase or decrease.

4. *Relationships between individual, phytocenotic and landscape levels.* Over a region with a lack of heat (such as the Boreal Forest) a warming promotes the growth of individuals, to a lesser degree increases the phytomass of each ecosystem (see item 1) and provokes fires at the landscape level, with possible stimulation or suppression of total phytomass pressure. The overall effect resulting from these changes can bring about either an increase or decrease in the phytomass of trees.

The above examples show that 1) Internal forest interactions, which incorporate causative relationships in the structure and dynamics of vegetation, should possess specific features for each vegetative zone and 2) the changes of the same global ecologic parameters can result in absolutely different alterations in vegetation parameters – forest area, forest phytomass, species composition, etc., for different vegetation zones (ecological conditions).

This situation, as well as general principles of simulation, bring forth the conclusion that a prediction model of Boreal forest should be hierarchical. As a first step in the description of forest dynamics within a certain type of landscape located on a climatically homogeneous territory, we can suggest a three-level "individual-phytocenosis-ecosystem-landscape" which, in general terms, could be written as

$$\dot{x} = f(x, y, \psi) \quad (1)$$

$$\dot{y} = g(x, y, \psi) \quad (2)$$

$$\dot{z} = h(x, y, z, \psi) \quad (3)$$

which is an analogue of a hierarchical model [Cherkashin, 1983], or a deterministic analogue of a stochastic model [Shugart, 1984]. In model (1-3) ψ represents ecologic parameters and, first of all, climatic parameters acting at the introduced levels; x – variables of an individual, in the simplest case

one linear size or the phytomass of an individual; y - variables of an ecosystem, in the simplest case numbers of the target tree species; z - variables of the territory (landscape), in the simplest case - sections of the territory occupied by different types of phytocenoses.

Out of the three introduced functions it is the organisation of f function in (I) that is best known. Usually it is an equation which describes the carbon balance for an individual

$$f(x, y, \psi) = F(x, y, \psi) - g(x, \psi) \quad (4)$$

where the first item describes photosynthesis the simulation of which is amply treated in the literature (this problem is far from being exhausted), and the second term represents the costs to the individual for various needs. Argument y in $F(x, y, \psi)$ describes changes in the amount of certain resources used in ecosystems due to a competitive interaction within phytocenosis. This relationship depends on the type of the resource for which plants compete, on the morphology of plants and their spatial distribution. Carbon spent by an individual g depend, in the first approximation, only on the state the individual itself, rather than on y .

Since variables y are the numbers of certain groups of individual trees, q -functions describe the dynamics from this stress. If we analyse a population of trees of the same species and the same age, function q will be equal to the individual's mortality. Unlike the theory of growth, the theory of this phenomenon occurring in perennial plants is but slightly developed, and, in simulations, one has to make use of empirical relationships. If we deal with a tree population of the same age which is divided into groups (usually in terms of size) or populations of different ages without reproduction, functions q will be still equal to mortality in respective groups, and the problem of deducing the right-hand parts of e.g. (2) remains basically the same. However, the task becomes quantitatively more intricate if we consider a population of various ages with reproduction. In such a case we come against a problem of age-related dynamics, and function q describes both fecundity and mortality. The theory of growth, reproduction and mortality required for such a case is practically non-existent.

The description of landscape dynamics by means of equation (3) is usually based on the idea discussed in Shugart et al. (1973) whereby the territory is divided into "cells", each occupied by an ecosystem in a certain state (stage of development); and the dynamics of sections the territory occupied by similar ecosystem (components of vector z) is described by Markov's linear system

$$\dot{z} = C(x, y, \psi)z \quad , \quad (5)$$

where matrix elements $C(x, y, \psi)$ are equal to frequencies of transitions from one state into another occurring during endogenesis (successional dynamics) and under the impact of external factors. The fact that the system is z -linear (e.g. (5)) means that we adopted the strong hypothesis according to which a cell's dynamics is independent of the dynamics of neighboring cells. Later in this paper, we shall use system (5) in a simulation example.

Now, after providing a general description of a hierarchically organised system (1-3), we shall discuss two examples of its application which correspond to situations described above.

1. Let us formulate a simple ecological-physiological model which accounts for the interaction of the individual and ecological levels. We shall assume that photosynthesis depends on one ecologic global factor, for example, on CO_2 , and designate $c = [CO_2]$. We shall assume that an ecological interaction is revealed in competition over a certain factor (resource) R , which also governs photosynthesis; it could be light, water, mineral elements. Other factors are implicitly incorporated into the models. Suppose, $R(y)$ is a unit amount of the resource (per unit of absorbing area S); it would be natural to suppose that without competition the amount of available resource is a maximum, $R(0) = R^{\max}$. We use the simplest, multiplying, dependence of unit rate of photosynthesis F on the introduced factors

$$F = bcR(y), \quad b = \text{const} \quad ;$$

this is a reasonable assumption bearing in mind that the estimations to be obtained will be approximate and comparative.

We shall study the simplest ecological system - a population comprising y individuals of the same age. Let S be the absorbing surface of an individual (leaf area or the active root system area), and m is its phytomass depending on S , $m = pS^w$ (actually $w > 1$). To obtain analytical results, let us assume that carbon spent by the individual in (4) are proportional to total photosynthesis, $g \sim SF$. Hence, the individual growth equation will be

$$\dot{m} = \tau_0 SF = \tau_0 bcSR, \quad \tau_0 = \text{const} < 1 \quad ,$$

or

$$\dot{S} = \tau S^\alpha R(y), \quad \tau = \tau_0 bc / pw, \quad \alpha = 2 - w < 1 \quad .$$

To obtain the strength dynamics equation we assume that the population is in an ecological optimum, so that mortality caused by unfavourable climatic factors is reduced to a minimum and one can suppose that it is caused only by competition; that mortality in (2) depends on the available resource via argument $W = R(y) / R^{\max}$, $q = q(W)$, with $q(1) = 0$, $\partial q / \partial w < 0$. In concrete calculations, for lack of a constructive theory, we use empirical relationships $q(W)$. So, we have in front of us an ecological-physiological model of the target object:

$$\dot{S} = \tau S^\alpha R(y); \quad \dot{y} = -q[R(y) / R^{\max}]y \quad . \quad (6)$$

Various hypotheses about the type of a limited resource, the morphology of the absorbing surface and spatial location of individuals yield a definite form $R(y)$ obtained either theoretically or by simulation. For example, if trees compete for water, of the individual's root system occupies a ring of area S , if the individuals are located on the plane independently of one another, and in the area where root systems overlap, water is distributed equally between all overlapping individuals, then one can show that function $R(y)$ is

$$R(y) = R^{\max}(1 - e^{-2\delta Sy}) / 2\delta Sy \quad (7)$$

where δ is an empirical factor which describes the extent to which root

ends fill the ring.

2. Experience obtained from concrete calculations with system (6) shows that in populations of trees which are long-lived, mortality caused by competition per unit time (1 year) is small enough, i.e. that W is close to 1. In such a case if we use (7), $\delta S y \ll 1$ will be fulfilled and

$$R(y) = R^{\max}(1 - \delta S y) \quad .$$

Then system (6) turns into

$$\dot{S} = rS^\alpha(1 - \delta S y) ; \dot{y} = -\beta \delta S y^2 ; \beta = \partial q / \partial R |_{w=1} \quad (8)$$

This system provides a qualitatively correct description of basic effects in the combined dynamics of an individual's numbers and size, and makes it possible to directly examine the effect of ecological damping of growth acceleration mentioned in 1.

First let us consider a case of tree growth, i.e. system

$$\dot{S} = rS^\alpha ; \dot{y} = -\beta \delta S y^2$$

Its solution, with initial conditions being $S(0) = S_0$, $y(0) = y_0$, is as follows:

$$S(t) = [(1-\alpha)rt + S_0^{1-\alpha}]^{\frac{1}{1-\alpha}} ;$$

$$y(t) = \frac{y_0}{1 - KS_0^{2-\alpha} + KS(t)^{2-\alpha}} ; K = \frac{y_0 \beta \delta}{r(2-\alpha)}$$

Bearing in mind that the phytomass of an individual is $m(t) = pS(t)^w$ we obtain

$$m(t) = p[(1-\alpha)rt + S_0^{1-\alpha}]^{\frac{w}{1-\alpha}}$$

$$M(t) = \frac{y_0 m(t)}{1 - KS_0^{2-\alpha} + K[m(t)/p]^{\frac{2-\alpha}{w}}}$$

In actual dynamics the system quickly forgets the initial value of size S_0 , which allows us to consider a simplified case when

$$m(t) = p[(1-\alpha)rt]^{\frac{w}{1-\alpha}} ; M(t) = \frac{y_0 m(t)}{1 + K[m(t)/p]^{\frac{2-\alpha}{w}}} \quad (9)$$

Now let us suppose that photosynthesis intensity has changed as a result of a change in the global CO_2 concentration $r' = r + \Delta r$, $\Delta r / r \ll 1$. From formula (9) one can find that

$$m(t, r + \Delta r) = m(t, r) \left[1 + \frac{w}{1-\alpha} \frac{\Delta r}{r} \right] ; \quad (10)$$

$$M(t, r + \Delta r) = M(t, r) \left\{ 1 + \frac{w}{1-\alpha} \frac{\Delta r}{r} - \frac{1}{1-\alpha} \cdot \frac{K \left[\frac{m(t, r)}{p} \right]^{\frac{2-\alpha}{w}}}{1 + K \left[\frac{m(t, r)}{p} \right]^{\frac{2-\alpha}{w}}} \right\}$$

As can be seen, the correction for M is less than that for m , which describes in the framework of the model, the effect under consideration.

The analysis of model (8) with the relationship between an individual's growth and competitive interaction, yields formulae similar to (10) where Δr depends only weakly on time (for the sake of brevity possible estimates for $\Delta r(t)$ are not cited here). Since the structure of dependence of m , M on Δr remained the same, the effect under consideration is preserved in model (9) as well.

To provide a model-oriented description of the next effect (item 4) let us look at a territory which is homogeneous from the viewpoint of soil and climate conditions. This means that landscape "cells" are occupied by ecosystems representing one succession line and differ only by the stage of development (age). Let us consider the situation [Spurr, Barnes and Barnes, 1981] typical for boreal forests, when a fire which completely or almost completely wipes out forests on some part of the territory, is the principal exogenic factor. New trees occupy this area, which results in the development of endogenic succession whose age count starts from the time of the fire. So, the formed cells are of pyrogenic origin; and their size and phase are determined by the state of neighbouring cells or by accidental factors which put an end to the fire. Since the notion "development stage" of an ecosystem is discrete, it is convenient to use the discrete analogue from system (5). Let us look at a simple case when the probabilities of being burnt down u_k for each state $k = 2, \dots, Q$ of the ecosystem, are equal and depend on one global exogenic factor $u = u(\psi)$. Duration of one stage will be chosen as a time unit. Then, the dynamics of those parts of the territory which are occupied by ecosystem at different succession stages $k = 1, \dots, Q$ will be described, for non-interacting cells, by the following system:

$$\begin{aligned} z_1(t+1) &= u(\psi) \sum_{k=2}^Q z_k(t) \\ z_k(t+1) &= z_{k-1}(t) - u(\psi)z_k(t) \\ z_Q(t+1) &= z_Q(t) + z_{Q-1}(t) - u(\psi)z_Q(t) \end{aligned} \quad (11)$$

Assuming that each cell is occupied by a population of individuals of the same age, one can describe its dynamics by the system (discrete analogue (6)):

$$\begin{aligned} S(k+1) &= S(k) + r(\psi)S(k)^a R(y) \quad ; \\ y(k+1) &= \{1 - q[R(y)/R^{\max}]\}y(k) \end{aligned} \quad (12)$$

where the rate of photosynthesis depends on the same factor ψ .

System (11-12) is an example of a three-level system of the "individual-ecosystem-landscape" type.

4. Let us assume that the territory, as a whole, is in a state of equilibrium, i.e. portions z_k are constant and equal $z_k^0(\psi)$. As factor ψ changes to $\Delta\psi$, the phytomass of a cell will become equal to

$$M(k, \psi + \Delta\psi) = M(k, \psi)[1 + W_M(k) \Delta\psi] \quad (13)$$

the probability of being burnt down

$$u(\psi + \Delta\psi) = u(\psi)[1 + W_u \Delta\psi]$$

equilibrium portions of the territory

$$z_k^0(\psi + \Delta\psi) = z_k^0(\psi)[1 + W_Z(k)] \quad (14)$$

Let us introduce the average phytomass per unit area of the territory

$$M(\psi) = \sum_k M(k, \psi) z_k^0(\psi)$$

which, in accordance with (13) will change following variations of ψ :

$$\mu(\psi + \Delta\psi) = \mu(\psi) + \Delta\psi \sum_k M(k, \psi) z_k^0(\psi) [W_M(k) + W_Z(k)] \quad .$$

Our purpose is to estimate the sign of correction for μ . Direct estimation $W_M(k)$ in (10) requires the setting of several constants and does not provide the desired accuracy. Let for concreteness ψ be mean temperature T . Let us try a simpler approach: it is known that in case of boreal forests the variation of $\Delta T = +1^\circ$ increases the rate of photosynthesis by 5–18%. Let us assume that this estimation is applicable to M (i.e., that the effect of ecosystem damping does not involve qualitative changes). Then

$$W_M(k) \approx 0.05 - 0.18 \text{ 1/grad (per grad)} \quad . \quad (15)$$

Probabilities $u(T)$, which have the order of magnitude of 10^{-2} 1/year for boreal forests, mostly change following the changes in the frequency of dry years. Analysis of corresponding data shows that when $\Delta T = +1^\circ$ the frequency of droughts for the European Territory of the USSR and Western Siberia will increase approximately from 0.3 to 0.4 1/year. Let us assume that probabilities u will increase in the same proportion:

$$W_u = (0.4 - 0.3) / 0.35 \sim 0.3 \quad (16)$$

With an accuracy requiring only slight corrections, stationary magnitudes from (11) are equal to:

$$z_k^0(T) = q(T)^{k-1} \frac{1-q(T)}{1-q(T)^Q} ; q(T) = \frac{1}{1+u(T)} \quad (17)$$

5. Let us look at a concrete situation – a pyrogenic cedar succession in Western Siberia [Sedykh, 1974], in which the ecological phytomass (ton/hectar) for twenty-year long stages $k = 1, \dots, 9$ is equal to

k	..	1	2	3	4	5	6	7	8	
M(k,T)	...	30	50	80	110	210	300	340	370	400

Let us assume that the probability of being burnt down during 20 years $u(T) = 0.2$. Calculations of z_k^0 and their derivatives yield the following expression for mean phytomass

$$\mu(T + \Delta T) = \mu(T) + 50(3W_M - W_u)\Delta T \quad .$$

As can be seen, the correction changes sign when passing through

$$3W_M = W_u.$$

Estimations W_M (15) and W_u (16) show that this ratio is quite reliable, i.e. the effect of phytomass growth at the ecosystem level has the same order of magnitude as the effect of its decrease at the landscape level.

EXAMPLE 2. GLOBAL-SCALE RESPONSE OF VEGETATION

At a global-scale, one approach to examining the possible changes in the size and areal extent of the world's forests is to use empirical models of climate and vegetation in a spatial context and to superimpose scenarios of climatic change. Emanuel et al. (1985) used the Holdridge life zone classification (Holdridge, 1947, 1964) to map the distribution of potential vegetation on the Earth's terrestrial surface. The Holdridge classification predicts expected vegetation as a function of a temperature and moisture index. By interpolating monthly temperature and precipitation data from 8000 meteorological stations onto a 0.5 degree latitude by 0.5 degree longitude grid and applying the Holdridge classification scheme to these data, Emanuel et al. produced a map of world vegetation. Each of the meteorological records was then altered by a change in the annual average temperature taken from Manabe and Stouffer's (1980) simulation experiment for a CO_2 -doubling. The initial procedure was then repeated to obtain a map of the potential vegetation to be expected after the climatic change.

In a subsequent critique of the procedure, Rowntree (1985) noted that the use of mean annual temperatures was less appropriate than the use of seasonally varying temperatures. It was also noted that it would have been more appropriate to use the difference between the $2 \times CO_2$ scenario and the General Circulation Model control run (rather than the difference between the $2 \times CO_2$ scenario and observed data) to derive the magnitude of the temperature changes from which to calculate the effects of climatic change on vegetation. Based on these criticisms, Emanuel et al. (1985b) revised the maps of the Holdridge life zones for both the base case (present-day conditions as reflected in the meteorological station data set) and the $2 \times CO_2$ scenario as shown in Table 1 (Shugart et al., 1986).

At a global scale, the life zone designations of 34% of the 0.5° by 0.5° grid cells were altered. In the higher latitudes, the generally higher temperatures resulted in a 37% decrease in the areal extent of tundra (see Table 1 in Emanuel et al., 1985). Boreal moist forest was replaced by cool temperate steppe and, to a lesser degree, by cool temperate forest and boreal dry bush. Boreal wet forest was replaced by cool temperate forest and boreal moist forest. The boreal forest zone shifted north and replaced about 42% of the 0.5° by 0.5° grid cells designated as "tundra" in the base case. The northern extent of the tundra was also increased.

Because the temperature changes in the Manabe and Stouffer scenario were smaller toward the equator, there were smaller changes in the tropical life zones. Nevertheless, the areal extents of the subtropical and tropical life zones increased by 8%. The area of subtropical forest life zones decreased by 22%, while the subtropical thorn woodland and subtropical deserts increased by 37% and 26%, respectively.

Table 1: Summary of Changes in Life-Zone Extents (10^6 km^2)

	Area	
	Base case	Elevated CO ₂
<i>Forests</i>		
Tropical:		
Rain	0.003	0.003
Wet	0.384	0.410
Moist	8.647	9.888
Dry	9.992	14.033
	19.025	24.334
Subtropical:		
Rain	0.014	0.020
Wet	0.496	0.261
Moist	7.947	5.767
Dry	3.506	3.329
Warm Temperate:		
Rain	0.029	0.021
Wet	0.562	0.494
Moist	7.766	5.990
Dry	7.456	8.185
	15.813	14.690
Cool Temperate:		
Rain	0.252	0.200
Wet	1.618	1.319
Moist	9.418	10.108
	11.287	11.627
Boreal:		
Rain	0.343	0.062
Wet	4.266	1.437
Moist	12.654	9.381
	17.263	10.880
<i>Grasslands</i>		
Tropical:		
Very Dry Forest	4.715	6.045
Thorn Woodland	2.351	3.144
	7.066	9.189

Subtropical Thorn Woodland	1.649	2.256
Warm Temperate Thorn Steppe	5.135	5.157
Cool Temperate Steppe	8.931	11.922
	22.780	28.524

Deserts

Tropical:		
Desert Bush	2.321	3.110
Desert	8.419	9.521
	10.740	12.631

Subtropical:		
Desert Bush	1.532	2.549
Desert	1.382	1.109
	2.914	3.659

Warm Temperate:		
Desert Bush	4.863	4.166
Desert	1.886	1.243
	6.748	5.410

Cool Temperate:		
Desert Bush	3.586	3.170
Desert	1.256	0.875
	4.842	4.044

Boreal:		
Dry Bush	1.282	2.576
Desert	0.027	0.015
	1.309	2.591
	26.554	28.334

Tundra

Rain	0.063	0.000
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Wet	1.770	0.472
Moist	2.636	2.504
Dry	0.000	0.058
	4.470	3.034
Ice	2.218	0.567
Total	131.372	131.368

Table from Emanuel et al., 1985.

In the analysis described above, precipitation was left unchanged and thus average evapotranspiration increased. If precipitation were allowed to change, however, a reduction of boreal forest would still result from the higher temperatures, according to the Holdridge life zone classification. Drier conditions would only further decrease the areal extent. Wetter conditions would allow the expansion of boreal forests into areas classified as "boreal desert" (Table 1), but the area of boreal desert is so small that these gains would do little to offset the reduction in boreal forests caused by warmer temperatures. In contrast, the proportions of grasslands (including thorn woodlands and thorn steppe) and deserts would be expected to change considerably under different precipitation regimes. Increased precipitation would have little effect on the area of tropical forests, but decreased precipitation would diminish the area greatly.

Emanuel et al. (1985) identified several sources of uncertainty in these sorts of assessments, including the choice of climate scenario, the choice of mapping algorithm and the relative coarseness of the data grid. Nonetheless, the simulated effects of a warmer climate on the areal extent of the coniferous boreal forests are not inconsistent with the conclusions one might draw from a casual inspection of the position of the boreal forests in relation to key temperature variables. Throughout North America and Eurasia, the northern limit of the boreal forest is delineated by the mean 13°C isotherm in July (Larsen, 1980). The southern limit of the forest is bounded by the mean 18°C isotherm in July in regions with favourable moisture conditions (where drier conditions prevail the limit is situated north of this isotherm). Although spatial correlations between climate variables and vegetation do not necessarily establish cause and effect, it is important to note that, with respect to growing season temperatures (indicated by the July isotherms), the boreal forest has a range of only about 5°C under favourable moisture conditions and less than 5°C under drier conditions. Thus, increases in average summer surface temperatures of just a few degrees, as projected by GCMs for a CO₂ doubling, might be expected to displace markedly the present boundaries of boreal forests.

CONCLUDING REMARKS

To conclude our discussions we would like to identify three themes that we feel are important with regard to the monitoring of the boreal forest. These are:

1. The usefulness of mathematical models to predict the longer term consequences of change in the boreal forest.
2. The apparent sensitivity of the boreal zone to change particularly to the current scenarios being produced by general circulation models for a climatic warming induced by CO₂ and other greenhouse gases.
3. The potential effect of the boreal forest on the global systems, particularly the global atmospheric balance of gases.

We will treat these three points in order.

1. Utility of Models

In this paper, we have introduced a substantial section involving the analysis of a model by Antonovsky and Korzukhin. This analysis identifies a central point that is important in the understanding of change in the boreal forest – *change in one level of a hierarchically-structured system, such as the boreal forest, does not translate at another level of the hierarchy as a change of the same magnitude or even of the same sign.* This point is clearly evidenced in the example case of a climate warming on western Siberian forest where a warming increased individual tree growth rates and increased regional wildfire rates. The magnitudes of these two processes, one that increases biomass and one that decreases biomass, were of the same order.

There is a general convergence of forest models being developed in the USSR and the USA in terms of the philosophy that underlies the modeling approach. We have presented a USSR example in this text and readers are referred to Shugart (1984) for a general review of a USA modeling approach. The point of convergence is that in both countries (as is also the case elsewhere), the importance of recognizing the age structure of the forest in formulating a proper forest dynamics model is being recognized and included in the models. In the USA-case, this recognition has been in the development of individual-tree based forest models and an emphasis on digital computer simulation. In the USSR-case, this recognition has been in the formal incorporation of age and size structure in non-linear systems of differential equations that describe forest dynamics. Thus, while the models have a common basis in philosophy they differ in their realization. We see comparisons across these approaches as a very useful scientific endeavour.

2. THE SENSITIVITY OF THE BOREAL ZONE TO CHANGE

In the present paper, we have shown results of a static mapping experiment using the Holdridge (1947, 1964) Life Zone classification and the Manabe and Stouffer (1980) climate-change scenario. This example identified the boreal zone as a focal zone for seeing change. We feel that these results should be explored using other classification systems. The Holdridge classification is based upon a logarithmic temperature \times logarithmic moisture classification. Since the boreal zone is in the part of this doubly logarithmic scheme that is small with respect to both dimensions, the sensitivity to change could be a consequence of scaling. Frankly, we doubt this is the case (based on the correlation between Holdridge classifications and other geographic vegetation classification schemes).

Eventually one would like to see an ability to develop dynamic equations of forest (and other ecosystem change) that would cover the domain of the Holdridge Life Zone space. One step in this direction could be an inter-comparison of vegetation in the boreal zones at a global scale using satellite-based, remote-sensing of the sort developed by Tucker et al. for the African continent. This mapping/reclassification work would involve a considerable degree of international cooperation.

3. THE EFFECT OF THE BOREAL FOREST ON THE GLOBAL SYSTEMS

But the boreal forest is not necessarily a passive player in the global change interactions. The work of Tucker and Fung reported in the last (1986) *International Congress of Ecology* points to a possible role of terrestrial ecosystems in controlling the annual oscillation in atmospheric CO_2 . This evidence is based only on correlation and is most convincing in the case of higher northern latitudes. The existence of correlation is not proof of the existence of a mechanism – but we would suggest that further studies of the effect of the boreal forest on the global atmosphere are certainly indicated by this work.

In the case of other trace gases (particularly methane), we see the processes of swamp formation and swamp reforestation as a function of climatic change as having a potential to change the percentage of the global surface that generates methane. The understanding of the global budgets of carbon-containing gases (carbon dioxide, methane, etc.) must of necessity consider the boreal systems (that contain almost 50% of the living carbon in the earth) to a considerable degree. It has been pointed out in the case of the tropical forest that the large rate of forest clearing should be slowed until the global role of this forest is better understood. It is also the case that the boreal forest, the vast woods that covers the northern part of three continents, may also have a major role in the functioning of global systems. The potential importance of the boreal forests at the global scale indicates that they should be better understood in the global context before they are greatly altered or cleared due to more regional or local considerations.

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