WORKING PAPER

A REGIONAL MODEL OF LONG-TERM WETLAND-FOREST DYNAMICS

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for Applied Systems Analysis

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Foreword

Wetland-forest dynamics is a subject of great theoretical and practical interest, particularly with respect to the boreal forest in the USSR, Scandinavia and Canada. Under current hydrological conditions, the characteristic time for succession from forest to bog (or vice versa) is about 100 years. But with greenhouse-gas warming of the atmosphere during the next 50 years, succession rates may be considerably altered, and this might have significant impact on the forest sector. It is therefore essential that models be developed and tested with historical data, so that an idea may be obtained of likely future states.

This Working Paper is a significant contribution to the literature on wetland-forest dynamics, and I commend Professor Antonovsky and his two colleagues in the USSR.

R.E. Munn
Head
Environment Program

Acknowledgement

The first author wishes to show his deep appreciation to Professor R.E. Munn, Leader, Environment Program, IIASA, for his overall support as well as his scientific help and advice. The first author also wishes to express his appreciation to Professor H. Shugart for most useful conversations.

Summary

We have tried to model in qualitative terms the dynamics of an entire forest and bog ecosystem which includes abiotic and biotic components. The former was the thickness h of the peat deposit and the latter was the fraction p of hygrophytes in the total phytomass. The dynamics of these two variables, modelled by formalizing the associated ecological mechanism, was the main line of this research.

The proposed model describes simultaneously the process mechanism for an ecosystem and its regional setting because it is referenced to basic types of ecological conditions to be found in the chosen area.

The bogging proceeds in two qualitatively different phases.

The first is exogenetic in that the system develops under the impact of exogenous forced watering which reduces aeration W. The characteristic time of climatically dictated bogging-debogging fluctuations range from several to 200 years. The horizontal bogging rates are as high as meters per year. In this phase $h < \Delta h$ and $W > W^*$; the value h is constant and stable with specified values of the ecological parameters W and T, of which W is more important and variable; this phase is associated with bogged forest. The state is labile and easily reversible in response to climatic variations in which $W > W^*$. The value of h varies quickly to fit W.

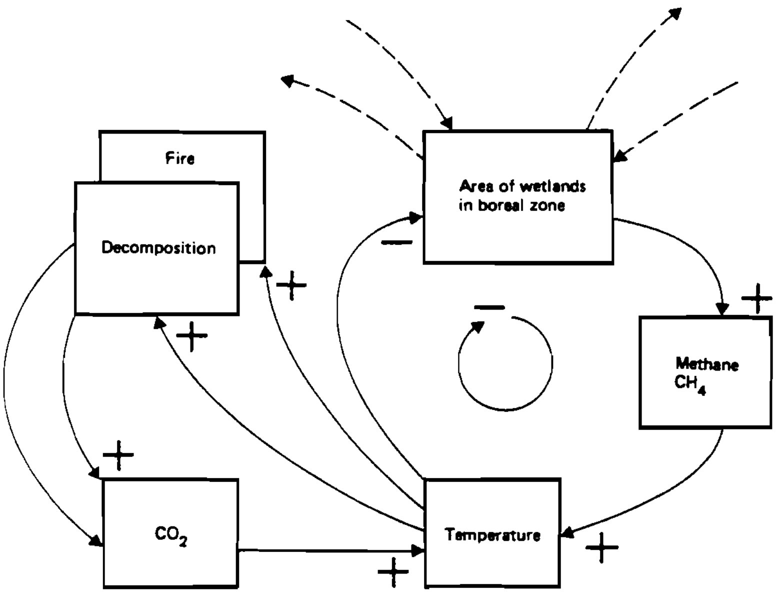
The second phase is endogenetic in which the gradual bogging fluctuates relatively little at a horizontal rate of centimeters per year. In this phase $h > \Delta h$, $W < W^*$, and the value of h is unstable and grows infinitely. The process is stable in that the climatic variations within the range $0 < W < W^*$ do not prevent the infinite growth of h. For this reason, the bogging is irreversible with usual climatic variations (against whose background exogenesis occurs) but is reversible over large time spans during which the bog ecosystems are influenced by the specifics of mire development, i.e., when regional aspects become important. The peat deposit and the impermeable horizon may be said to be the "memory" making the system stable. The exogenous watering effect may be reduced with peat accumulation preserved. This phase covers the remaining part of the hydromorphic series in the exogenetic succession of marshy forest → treed bog → open bog → lake-and-bog complex.

Recommendation

In spite of differences in the structure of boreal and tropical forests, both types are greatly influenced by climate and by the concentrations of the chemical constituents of the atmosphere. In turn, both types of forest can influence climate and the atmospheric concentrations of trace gases, e.g., through the "greenhouse" effect (forests store large amounts of carbon dioxide and other trace greenhouse gases).

Adopting the point of view of, for example, G. Zavarzin and W. Clark, methane (CH_4) released from the wetlands of the boreal zone is sufficiently large (hypothetically its effect is approximately 1/3 of that of the other trace gases) to affect global warming, which will occur in the boreal zone also. Then a negative feedback chain appears: wetland → methane → warming → less wetland (due to more evaporation) → less methane → cooling, thus helping to stabilize the climate system (maybe even on a regional scale). Whether other greenhouse gases act in a similar way is unknown to the authors. At the same time, however, the increase in temperature would result in a higher rate of biological activity and a shorter "frozen" winter, leading to higher methane releases in both cases. It would be interesting to study these feedbacks within a long-term monitoring program. Of course, it will not be simple to make quantitative calculations for climate purposes: let us suppose that we know how much CH_4 is emitted from 1 km^2 of swamp or wet forest, and that we can infer the resulting decrease of area of such wetlands. But, for calculations of the CH_4 balance in the atmosphere, we also have to know the fluxes and decomposition rates in the ocean and soils.

The negative and positive feedbacks occurring in the methane/greenhouse warming process are illustrated schematically below. A main recommendation of this report is that these feedbacks be studied both through the construction of models and the development of appropriate monitoring systems.



A REGIONAL MODEL OF LONG-TERM WETLAND-FOREST DYNAMICS

M.Ya. Antonovsky, F.Z. Glebov and M.D. Korzukin

INTRODUCTION

In strongly watered taiga lowlands of boreal forests, the woodland and wetland are the prevalent component of the landscape. Large areas are covered there by intermediate ecological types such as treed bogs. In particular, in the taiga zone of Western Siberia automorphous (dry site) forests, open wetlands, and intermediate treed bogs, each take up one third of the total area (Glebov, 1984; Gorozhankina, Kostantinov, 1983; Vegetation of the West Siberian Plain, 1976).

A description of the landscape dynamics in such an area would be useful for both research and application purposes. (As usual, endo- and exogenous descriptions will have to be compiled; see below). Such a description should cover the dynamics of area fractions taken up by different ecosystem, or landscape, types and variations of these dynamics in response to the most usual events in the area.

These are aspects of the general issue of environmental stability. When a climatically uniform area is viewed as a regional entity, then the variety of landscape (or ecosystem, or biogeoecological) entities influences:

- the water budget (when averaged over fairly long periods $t \sim 10^2$ - 10^3 years, forests have a zero budget and bogs a negative one, because they accumulate

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water);

- the carbon budget (over the same periods, forests have a zero CO_2 budget and bogs a negative one because they accumulate the organic matter);
- The CH_4 balance (forests produce much less methane than bogs do).

The intermediate type, treed boglands, is intermediate in terms of these properties. These parameters make a strong impact on the climate while the landscape dynamics are strongly dependent on the climatic parameters. Consequently, over-watered taiga areas should be a special entry in the list of climatic types to be used in environment models (Krapivin, Svirezhev, Tarko, 1982). In a similar way, in calculating the shifts of vegetation zones in response to the expected climatic changes (for example, greenhouse warming), the treed bog should be recognized as a type of landscape and so the use of purely forest models will have to be expanded (Emanuel, Shugart, Stevenson, 1985).

OBJECTIVE, MODELS, GOALS OF MODELING

1. *Objective.* The goal of this research is to obtain a uniform description of an ecological series arranged in increasing order of hydromorphism, ranging from automorphous forest to open bog. In the general case, the bogging which starts in some point of an area goes through this series in a so-called ecogenetic succession (Sukachyov, 1975; Razumovskiy, 1981). The characteristic time of this succession is $\tau_0 \sim 10^3$ years; in other words, the processes are fairly slow as far as observation by one researcher or even the lifetime of science is concerned.

The first task is to find an ecosystem on which sufficient qualitative and occasionally quantitative knowledge is available. The basic force which results in the succession of ecological types is peat formation (or destruction in the case of debogging).

2. ***Model type.*** A model is a set of physically, ecologically, etc., interpretable variables linked through causally interpretable relations in some "model language" dictated by the particular system, our knowledge of it, and the goal of modeling.

According to a recent survey of wetland models (Mith et al., 1982) and the data of a symposium (Using Mathematical Modeling .., 1984), there are numerous models which describe various aspects of material and energy cycling and the ecological dynamics in the forest-bog system. Most of these models are simulation types in that they represent simultaneously numerous variables and attempt to provide a quantitative description of their dynamics over relatively short periods, tens of years. They simulate specific ecosystems or small bogged areas. Our system which consists of treed bogs of various ranks is different in that its characteristic periods are much longer; further, these ecosystems function in a broad range of ecological conditions.

In our model the number of variables is reduced to a minimum in order to represent in a concise and illustrative way the basic regularities in the forest-bog interaction and the succession of ecological types while unimportant details are left out. The variety of current ecological simulation models is much wider but simple models are useful as research tools. If necessary, the proposed simple model could easily be expanded.

The characteristic time τ over which the dynamics of some process is studied has its own list of variables and consequently, mechanisms. Variables for which $\tau_i \ll \tau$ converge quickly to equilibrium values that depend on the current values of the basic variables or, in the case of oscillations, of averages. In our case this is true of the adjustment of the peat bog mineral flux to the unconfined groundwater head (τ_1; similarly, for the atmospheric flux (τ_2): growth and lifetime of an individual tree, grass plant, and moss; vegetation litter and litter decomposition (τ_3). The order of magnitude of all these τ_i is $10^0 - 10^2$ years.

The variables for which $\tau_i \gg \tau$, are viewed as constant! These are tectonic shifts and geomorphological processes.

Climatic changes may probably occur over the entire range of characteristic times.

As noted above, the basic characteristic time of our system is the peat formation time, $\tau_0 \sim 10^3$ years. Consequently, the least sufficient dynamics description would need a single dynamic variable, the remaining variables being either slower or faster.

3. Goals of modeling. The overriding goal is to determine the list of variables and their interdependencies describing the mechanism of forest-bog interaction and alternation. The modeling technique is viewed as a way of compressing the available data and deriving the basic dependencies which describe system structure.

In addition, the model will be helpful in a regional forecast of forest-bog dynamics. Representation of various states over the areas is dictated by the terrain, hydrology, and the rate of succession in the state space of the system variables. One of the modeling results is the association of pointwise models to specific conditions in the area with indications of the direction and rate of the forest-bog-endo- and exo-genesis. With the stage of development known for the ecosystems in the area and given the causally-interpretable model of their dynamics, the changes of ecosystem states in response to specific impacts such as climatic changes, drying, deposition of minerals from the atmosphere, etc., can be forecast.

In the discussion that follows the ecological mechanisms of initial bogging and the subsequent forest-bog dynamics that the model needs will be described; ecological variables will be introduced; a model will be devised; and its operation for the case of initial bogging and then for the entire ecogenetic succession will be described. In illustrating the potential of this approach, a similar model will be devised for lake bogging. See Appendix 1.

THEORETICAL MODEL CONSIDERATIONS

1. General. First, the forest and bog have to be defined.

According to Morozov (1926), the forest is a community of trees which act on one another and the environment; as a result, both the trees and the environment change. In ecological classifications, the forest is a vegetation type.

The bog is defined as a type of abundantly watered surface which is, as a result, covered with specific vegetation and where a specific soil process results in peat formation. The abundant watering, an abiotic factor, is the chief ingredient, the vegetation being secondary and represented by various types, including forests.

Consequently, in the most general terms the modeling of forest and bog alternations is impossible because the former is a vegetation type and the latter, a landscape type, the former being part of the latter.

Modeling is, however, possible in ecosystem terms. In the forest zone, the bogs are peat, as a rule; so the bog ecosystem can be defined as a hydromorphous system which accumulates water and is organically imbalanced because the rate of accumulation of dead organic matter is faster than decomposition resulting in peat accumulation. Similar definitions of an entire bog rather than a bog ecosystem have been provided by various authors (Moore, Bellamy, 1973; P'yavchenko, 1974; Boch, Mazing, 1979). In a similar way, an automorphous forest may be defined as an ecosystem in which organic matter and water input and output are balanced because the dead organic matter arrives and decomposes at the same rate while incoming water is removed by transpiration and runoff. These properties of forest and bog ecosystems are true of time spans equalling hundreds or thousands of years; nonstationarities whose characteristic times amount to hundreds of years such as the phytomass dynamics and related hydrological variations are smoothed and neglected.

The primary cause of these differences is abiotic, viz. the different watering of the soils. The mechanism which brings about differences in system functioning is biological and is shaped by the specifics of vegetation ecomorphologies and " ... the biological rotation of substances in the phytomass" (Glebov, Toleiko, 1975). Let us show this for a marshland forest.

Such forests consists of trees, shrubs, grasses, and mosses. Peat is formed chiefly from the dead underground parts of vegetation decaying anaerobically.

Unlike shrubs and hygrophytes, the above-the-surface part of trees is much larger than the underground part and accounts for up to 70 percent of the phytomass. Because the trace element nutrient (ash) content of wood is insignificant and trees live for a long time, the contribution of tree trunks to biological rotation and peat formation is not large whereas the litter which mineralizes quickly, supplies trace elements and nitrogen in sufficient quantities to accelerate peat decay, concentrate the trace elements in the surface area of the peatland, stimulate biological cycling, and reduce the peat accumulation rate.

On the other hand, hygrophytes consist of grass biomorphs whose underground parts have a mass exceeding that of the above-the-surface parts and of mosses whose litter is insignificant, the growth occurring in the tops of stems with simultaneous gradual withering of the underground parts. Therefore, hygrophytes tend to retard peat decomposition, move the trace elements along the vertical profile of peatland, suppress biological cycling, and facilitate peat accumulation. Oligotrophic undershrubs decompose quickly* and so do not contribute to peat formation and, because of their high trace element content, to the biological cycling.

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* The high rate of decay is believed to be dictated by the low content of undershrub tissues in peat, which follows from the existing classifications of peat kinds (Tyuremnov, 1976) according to botanical peat analysis.

In effect, trees accelerate forest formation and hygrophytes accelerate bog formation.

In highly trophic conditions, the bog forests consist of species whose phytomass is nutrient-enriched and whose littler mass is significant, which accelerates biological cycling and peat decay. Therefore increased tropic content of soils favors and weakens bog formation, thus offsetting overwatering.

The latitudinal variations in climatic heat supply have the same effect because higher temperatures during the growth period also speed up biological cycling and the peat decay rate. In the forest zone, forest formation is facilitated and bog formation is hindered southward in the strip between the southern boundary of permafrost and the northern boundary of high soil salinity, or in the region covered by the model. Permafrost and the thermocarst it induces to the north of the forest zone perturb the natural course of exogenetic successions while soil salinity to the south hinders forest formation.

Plants can exist on wet peat soil by lowering the water table below the root layer during the growth period (variable water condition) and/or high water discharge. Trees are known to be sensitive to shortages of oxygen in the soil and so a rise in the water table and reduced water discharge favor hygrophyte settlement and force trees out.

Between the automorphous forest and bog there are numerous intermediate transitory states which can be viewed as the following ecosystem types; automorphous forest, AF; marshy forest, MF; bogged forest, BF; treed bog, TB; open bog, OB; and regressive lake-bog complex, LBC. These will be referred to as development phases. They are reversible,

The extreme phases in this succession, AF and LBC, are relatively stable in the face of exogenous factors because their biological cycling is balanced.

For FA, this balance follows from its definition. For LBC the peat accumulation is offset by its destruction as a result of lake formation. LBC is the climax of bog formation because possible further evolution culminates in replacement of the bog by another landscape component, a lake.

All other phases are unstable. The instability results from imbalance of the biological rotation and peat accumulation, which, as in the case of FA, follows from the definition of a bog.

2. *Bogging mechanism.* The ecological mechanisms for the initial bogging stage should by all means be represented in a model describing the triggering process. There are two different bogging mechanisms.

A. Oligotrophic high-moor bogging by atmospheric waters, phreatic groundwater, temporary perched groundwaters, and waters of advancing high-moor bogs, Figure 1. (All the variables in Figure 1 will be described later.)

The initial state, FA, is balanced in terms of mineral and organic rotation. As a result, the forest is littered by partly decayed organic layer $h = h^{\min}$ thick. What is important is that this equilibrium is stable. For instance, a temporary increase of the litter causes an increased decay rate and the system returns to the state in which $h = h^{\min}$.

When the exogenous conditions change in an area taken up by FA, the soil is watered. The excessive watering reduces the aeration and decomposition of the withered organic matter. Simultaneously, hygrophytes, in particular, peat mosses which are the chief contributors to peat formation, enter the ecosystem. As a result, the litter thickness, h, increases.

As h increases, a impermeable horizon forms in the soil to inhibit water infiltration and increase the stagnation. Until a certain time, as long as the chief component of the system is a labile living organism, the process can easily be reversed by climatic fluctuations. In dry years when the average water level drops, the or-

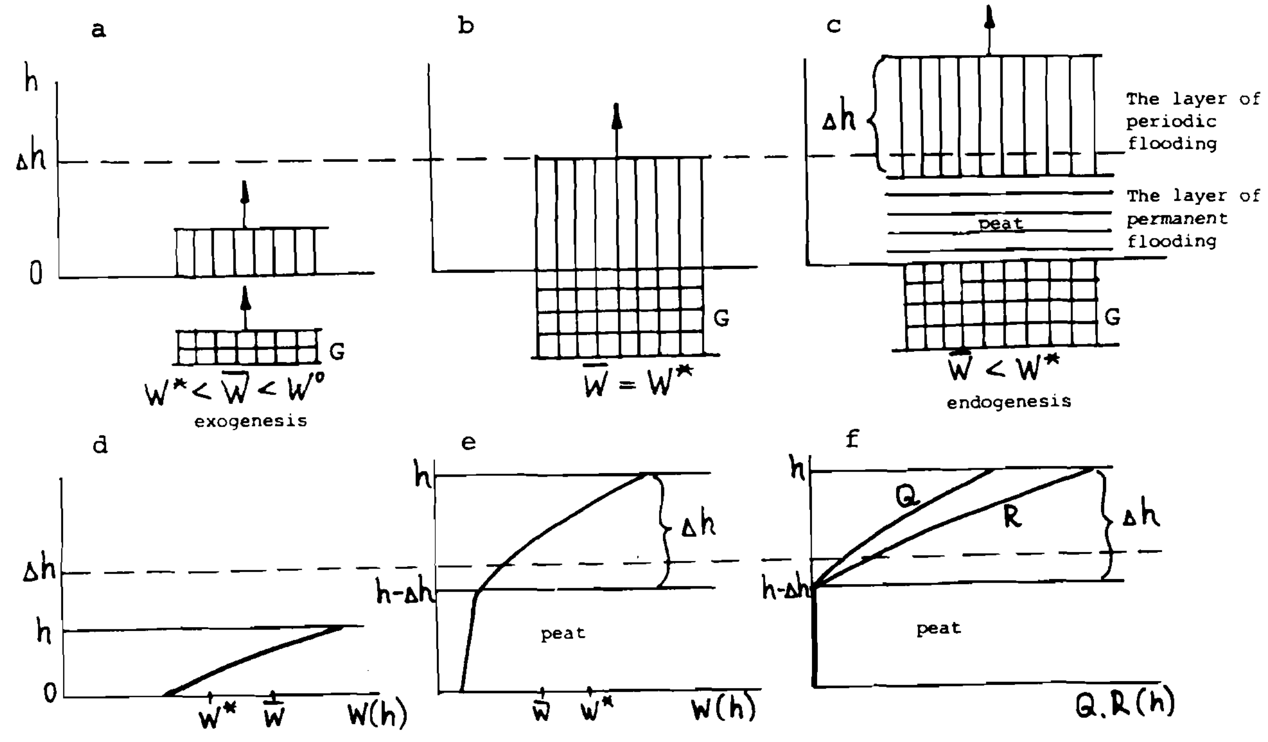

Figure 1 Genesis of the peat-generating layer and the alluvial horizon. Q- inflow of withered phytomass; R - rate of its decay; Δ h - thickness of the peat-generating layer; G - thickness of the impermeable horizon; W - aeration; W^0 its initial value; $\bar{W}$ - value averaged over the peat-generating layer; W^* - boundary value marking replacement of exogenesis by endogenesis; a - start of the process; b - critical time when h = Δ h, $G=G^{max}$, and $\bar{W}=W^*$; c - subsequent dynamics; d, e and f - vertical profiles of W, Q and R.

ganic accumulations decompose quickly. This is also true of the alluvial layer. Once the anaerobic condition is eliminated, it oxidizes. The characteristic time for this dynamic process is equal to the time over which the peat-generating horizon forms; see below.

This type of forest bogging is very widespread in the taiga zone, especially in its northern part and has for a long time been attracting attention. In his article "Bogs, their formation, development, and properties" Suyachyov (1926, p.34) wrote, "In numerous northern settlements one can hear the outcry that moss creeps onto the ploughland, meadows, and forests, that bog is now where quite recently was cultivated land. This process goes on literally before one's eyes in numerous locations". Sphagnum mosses grow at a rate as high as 10cm annually (Tyuremnov, 1949). As a result, dry sites become bogged at an annual rate of meters. The observations are scarce. According to Sparro (1924) the rate is 11 meters and according to L'vov (1976) one meter. P'yavchenko (1979, p.12) who gave much attention to reversibility of this kind of bogging wrote "... over 70 percent of the entire bogged area are lands peated to a little extent and overwatered temporarily".

The organic layer is inhomogeneous. Its decay increases downwards but until a certain thickness is reached, even the lower parts are not real peat and the tree roots are in mineral ground.

The system does not change before the following events occur which spell replacement of marshy forest by bogged forest:

1. An alluvial impermeable horizon forms, which results in a new, higher water table independent of ground water supply and temporary perched ground water.

2. The thickness of the organic layer whose lower part is real peat is equal to the variation of the new water table averaged over many years. This variation specifies, according to Ivanov (1975), the thickness of the peat-generating horizon Δh . In its lower part, water is nearly always present and its aeration W is minimal while the upper part is rarely watered and the aeration is maximal, which results in an organic decay rate gradient, or peat accumulation, see Figure 1.

3. The tree roots have been torn from the mineral ground; combined with the increased fraction of hygrophytes in the ecosystem, this results in a weakening of the tree stand and worse taxanomic indicators. The peat accumulation is therefore

suppressed by the litter and the total evapotranspiration to a lesser extent.

These phenomena make peat accumulation irreversible for the usual current climatic fluctuations. The system can be said to have gone through the exogenesis phase when its evolution had to be sustained by continuous watering and entered the endogenesis phase at which this exogenous impact is not needed any more and possibly does not exist because the ground water supply is made impossible by the gleyic horizon. The water table fluctuations above the gleyic horizon no longer inhibit the irreversible growth of h.

B. The other type of forest bogging is much rarer, occurring chiefly in the south of the taiga zone in river valleys. It is purely eutrophic (low moor) bogging by a high water table or running waters, and does not involve sphagnum mosses; instead the dying tree roots and grassy hydrophytes are chief contributors to the well-decayed woody and grassy-woody peat. With ground water supply, the variation of the water level and thus of Δh is much smaller than in the case of a phreatic atmospheric supply. In effect, the water table variability is no longer the necessary condition for alternation of aeration and lack of it for the formation of incompletely decayed vegetation residues that make peat. The amount of oxygen necessary for peat formation is brought by the running waters. Another cause of reduced Δh is the large amount of high content of tree litter nutrients which is decomposed by microbes quickly and completely. As a result, the acidity is decreased and microbiological processes are reduced.

C. There is a third type, very common in Canada - cutting a forest reduces evapotranspiration and raises the water table, leading rapidly to bogging.

The upper peat layer in micro elevations of the terrain has been shown (Glebov, Aleksandrova, 1973) to be saturated with aerobic microorganisms in an oligotrophic (ombrotrophic) bogged forest whereas in an eutrophic forest with its pressurized ground water supply where the water level and Δh variations are nearly unnoticeable, the peat layer contains the largest amount of such microorganisms in waterered macro depressions. In a eutrophic forest, the biomass and nutrient content of the tree litter is much higher than in an oligotrophic forest (Glebov, Toleiko, 1975). Tyremnov (1975) who had analyzed a large body of reported data noted that the thickness of the peat-generating horizon receded as the bog trophic content increased.

As in oligotrophic bogging, in the eutrophic case a gleyic horizon forms but the pressure prevents it from becoming continuous. The forest gradually bogs under the impact of this head. The exo- and endogenic stages of bogging cannot be distinguished. Because with high trophic content the peat accumulation is hindered, much weaker aeration is sufficient to trigger bogging than in the oligotrophic case.

In between these two extreme types, the several intermediate types differ in the formation conditions and, consequently, in the value of Δh.

A few quantitative characteristics might provide an insight into initial bogging. The peat increment results from the diverse processes of accumulation and decomposition of the withered phytomass. In exogenesis, the high aeration value accelerates the two processes, which immediately respond to variation of W; a bogged area can debog completely with normal climatic fluctuations. In endogenesis, the bogging is slow, gradual, and steadfast; the same fluctuations may diminish but never put an end to peat accumulation.

The time during which the peat generating horizon forms may be approximately determined if ΔH is assumed to form at the peat accumulation rate averaged over the Holocene. Radiocarbon measurements in various regions of the boreal zone (Bogs of West Siberia, 1976); Neishtadt, 1977; Ilomets, 1980; Glebov et al. 1980; Yelina et al, 1984; Aaby, Tauber, 1975; Zurek, 1976; Zoltai, Johnson, 1985) suggest that, depending on the bog types and for different Holocene periods, the peat formation rate varied from tenths to 1.5 - 2 mm/year and can be assumed to average 0.5 mm/year. The average Δh for a bogged forest in oligotrophic conditions is 40 cm with the tree roots staying in peat rather than in the mineral subsoil. Formation of a full peat generating horizon is seen to take $\tau \sim 800$ years. A gleyic horizon should also form within that time. The surface slopes in marshy and bogged forest are 0.01 - 0.02 (Ivanov, 1975). Consequently, with a peat accumulation rate of 0.5 mm/year, the bogging (peating of such slopes in the vicinity of bogs is 2.5 - 5 cm/year). In endogenesis, the (horizonal) bogging rate is two orders of magnitude slower than in exogenesis which is as high as meters/year. In 800 years the bogged forest would extend its boundaries by as little as 20 to 40 m. This is approximately equal to the width of a strip taken up by a peat generating horizon in a slope (40 cm/0.01 - 0.02 $\simeq$ 20 - 40m).

What is important is that the elementary processes contributing to bogging are interconnected through several feedback loops, in particular:

1. The larger the amount of sphagnum mosses in phytogenesis, the higher the soil acidity, the higher the rate of alluvial horizon formation, the wetter the litter and the weaker its aeration, and the larger the amount of sphagnum mosses.

2. The higher h, the lower the trophic content (because of the lack of supply from the subsoil), the weaker the stand of trees, the stronger the state of sphagnum mosses and the higher the peat accumulation rate, or the h growth rate.

CHOICE OF VARIABLES

Choice of variables is a largely informal procedure. In brief, the choice of variables was dictated by the following reasoning. Because the proposed model is qualitative, the fewer the variables the better, provided that you are lucky enough to pick the right variables!

Like any other ecosystem, our system should be described by both biotic and abiotic variables. Because the interdependence of tree and bog vegetation had to be described, the biotic variables should be m_1 and m_2, biomasses of hygrophytes and trees per unit area. Their values depend on the climate and local conditions; their simultaneous dynamics cannot be described unless the actual succession over time periods approximately equal to the lifetimes of trees and hygrophytes, or nonmutational successions are described (see Sukachyov, 1975; Razumovskiy, 1981). We are, however, interested in characteristic peat accumulation times and such an unduly detailed description of the system would be redundant. For our purposes, a concise description of the vegetation state of one biotic variable

$$p = m_1 / (m_1 + m_2) = m_1 / M \tag{1}$$

of the fractions of hygrophytes in the phytomass stock was found to be an illustrative indicator of the forest-and-bog system state; see below.

From the definitions of a forest and bog, it is obvious that the cause of p variations is variation in the thickness of the peat deposit or the litter, h. There is, however, no physical, ecological, or other way to detect a direct causal link between p and h. Intermediate variables are required which would "transfer the effect" of increasing or decreasing h on the value of p. According to our view of root layer ecology, the basic variables of this kind (essentially described in the second section) are trophic content T and humidity (more specifically, aeration) W. They are related to h through the hydrological conditions, especially the distance from the water table. Consequently, the model characterizes the water supply and the mineral supply in terms of one variable each. This approach dictated the introduction of variables and the relationships amongst them.

Now let us proceed to a complete description of the variables.

1. p is the fraction of hygrophytes and undershrub in the total stock of living matter in the living phytomass of the ecosystem, the fraction of wood being 1-p.

The processing of our data (Glebov, Toleiko, 1975) and that reported in the literature (P'yavchenko, 1967; Kazimirov, Morozova, 1973: Medvedeva et al., 1977; Kozlovskaya et al., 1978; Vakurov, Plyakova, 1982) has revealed that, depending on specific ecological conditions, the magnitude of the wood dry matter and of hygrophytes and undershrubs varies over a wide range. The fraction of hygrophytes and undershrubs was found, however, to be fairly stable in the total phytomass stock for every phase of development and so the values of p at this phase are for BF 0 - 01; for MF 0.1 - 0.5; and for TB 0.5 - 0.9. No data on BO or LBC have been reported because the stock of wood at these phases was not determined and it was assumed for BO that $p = 0.9 - 0.95$ and for LBC $p = 0.95 - 1.0$.

The fraction of hygrophytes is the basic variable; all other variables were introduced to explain this variable.

2. W is soil aeration, or O_2 concentration in the root layer. The degree to which ecosystems are hygrophilous is generally determined from the water content in the root layer of the peat deposit (Tyuremnov, 1976). This indicator is, however, inapplicable to such an important phase as bogged forest because the roots in such a forest are in the mineral subsoil whose water consumption and, consequently, watering are different from those of peat. Trees can exist on a watered peat soil if the wood risosphere receives enough oxygen while the metabolism products are removed, which occurs (a) when the soil waters go below the risosphere during the growth period (variable water supply) and/or (b) during high water flow rate. In the former case, the watering and aeration correlate and in the latter case they do not. There is a certain minimal value of aeration W^{min} below which plants cannot exist.

3. T is the root layer trophic content, or supply of nutrients. The trophic content indicator in our research was the ash content of peat as a percentage of the total dry weight of peat generators vegetation obtained from processing the

data reported by Tyuremnov (1976). The vegetation groupings specified by Tyuremnov and associated with certain kinds of peat with their characteristic chemical indicators were compared with our units of the ecosystem state which were the development phases of the exogenetic succession so as to calculate the ash content range for the root layers, Table. 1.

Table 1: Ash content, in percent, of various peat grades for phases of exogenetic succession.

Phase		Low-moor peat	Intermediate peat	High-moor peat
BF	0.0 - 0.1	-	-	-
MF	0.1 - 0.5	15.0	5.0	3.5
TB	0.5 - 0.9	8.0	4.0	3.5
OB	0.9 - 0.95	6.0	3.5	3.0
LBC	0.95 - 1.0	-	-	-

Remark: Because peat researchers classify areas where the peat layer is over 30cm thick as bogs, there is no data available on BF.

Three kinds of trophic content were used in our research, eutrophic (ash content five to 18 percent), oliogotrophic (ash content two to five percent), and dystrophic (one to two percent). With $T < T^{min} \leq 1\%$, the plants are assumed to be incapable of survival.

4. h-the thickness of a peat deposit does not need any justification. Its minimal value h^{min} stands for the litter thickness in an automorphous forest.

MODEL CONSTRUCTION

For a model to be developed, the key interdependencies of the variables have to be described and given a causal interpretation. In ecological modeling, several mathematical tools are used for this purpose.

If little knowledge is available, or these variables are too numerous, or random exogenous noise is strong, a statistical description such as that of Puzachenko and Skulkin (1981) becomes a natural tool. This approach makes all the variables into a totality of faceless "factors" and neglects the causal links; only the results of a statistical description can be in some way cautiously interpreted. In our case, the variables h, T, and W on which the dynamics p(t) are dependent cannot be regarded as quantities of equal importance. Unlike T and W, the thickness h of a peat deposit cannot make a direct impact on the vegetation state. Furthermore, the statistical approach is realistically applicable only to linear relations. In our case, however, significant nonlinearities are quite natural. In effect, a statistical approach would not work in developing our model.

We chose a model in the form of differential equations which make it possible to introduce and give causal interpretations of linear dependencies. Such equations describe the dynamics of the means, and the deterministic "kernel" of a noisy process making it possible to recognize the impact of random factors, notably climate.

The model represents the following dependencies as functions of appropriate arguments that will be shown graphically in qualitative terms. The characteristic peat formation time will be represented as τ_0.

1. *T as a function of h.* As h grows, the groundwater head drops, the inflow of alluvial and deluvial waters recedes, and the peatland receives water from the atmosphere. The ash content of the vegetation on the peat surface naturally drops with T.

The current value of T depends on a) removal of nutrients from the soil; b) the inflow of nutrients with underground, atmospheric, and river waters; c) removal of these substances when the peat deposit conserves and water flows out of the peat land. The rates of the first two processes depend on h because as the peat layer thickness increases the roots are separated from the mineral subsoil while the ground water supply changes for the atmospheric water supply. Let us denote the rate of nutrient inflow as $m'(h)$. The outflow rate is proportional to T. Consequently:

$$\dot{T} = m'(h) - \frac{1}{\tau_T} T = \frac{1}{\tau_T}[m(h) - T] \tag{2}$$

(factors which convert percentage into g/cm^3. sec are assumed to be introduced in (2)). Because $\tau_{\dot{T}} << \tau_0$ over $t \sim \tau_T$, the values of T are adjusted to the current values of h, which leads to a direct functional dependence

$$T = m(h)\,, \tag{3}$$

which is shown in qualitative terms in Figure 2. The shape of this function varies with the peat land and depends on the ground water head and amount, terrain, and the amount and kind of precipitation. In the general case, T(h) is a monotonically decreasing function. At the dystrophic stage in the peat deposit evolution when water arrives only with rain and snow, T ceases to depend on h (Figure 2b). In the case of a strong head, T does not fall as h increases (Figure 2c).

2. *W as a function of h.* The mechanism of the formation at the current values of W is almost the same as T. The 0_2 flow is the only exception: 0_2 is removed with water and consumed for oxidization of organic matters. If the rate of the latter process is proportional to the volume of the 0_2 flow then, as in the case of T, we have an equation:

$$\frac{dw}{dt} = \dot{w} = \frac{1}{\tau_w}\,[g(h) - w]. \tag{4}$$

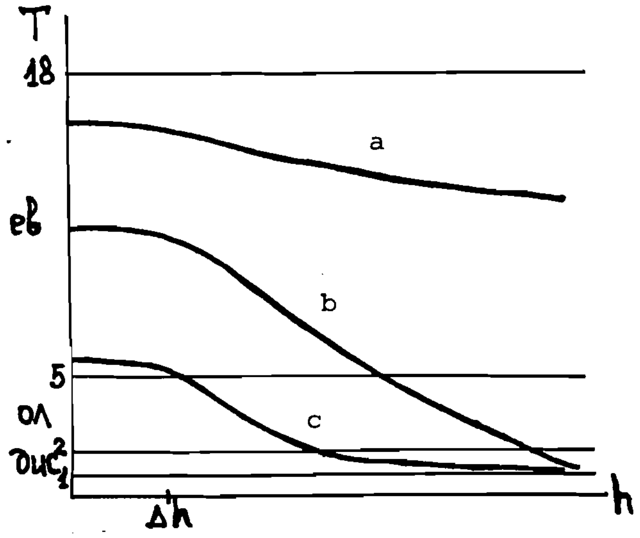

Figure 2: Trophic content versus peat deposit thickness: a - average case; b - tendency to stationary value corresponding to the amount of precipitations; c - strong head supply.

Since $T_w << T_0$, we have a direct functional dependence

$$w = g(h) \tag{5}$$

shown in qualitative terms in Figure 3. If the water supply is atmospheric and the bog surface is flat, then the aeration is low and does not depend strongly on h, see Figure 3.I. If the water is unconfined ground, alluvial or deluvial, then W is large and strongly dependent on h, see Figure 3.II.

3. *The dependence of the forest-bog succession phase (specified as the value of p) on the ecological parameters W and T.* As noted above, the dynamics of this dependence has two characteristic times:

a) τ_p , the time of succession (demutation) which follows a dramatic disruption of the vegetation state by fire, wind break, tree cutting, or defoliation by a forest

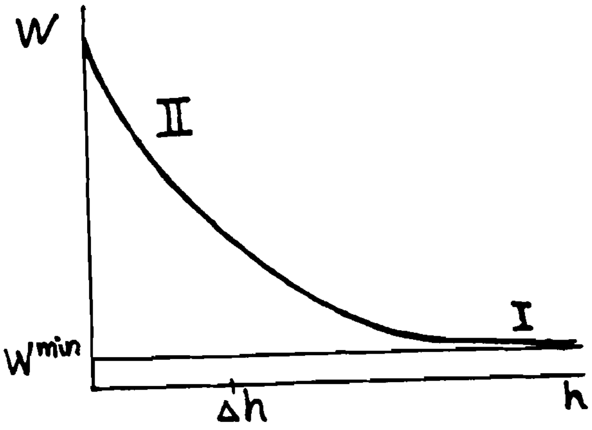

Figure 3: Aeration versus peat deposit thickness. I-atmospheric supply; II - ground water supply.

pest. This time is equal to the time of reaching the pseudoclimax which is a function of W and T, which, in turn, are dependent, in our view, on the current value of h. Numerically, τ_p is estimated from the lifetime of long-lived trees, which amounts to about 10^2 years.

b) τ_0, the exogenesis time, about 10^3 years, $>> \tau_p$.

In formal terms, the demutation dynamics p is described by the equation:

$$\dot{p} = \frac{1}{\tau_p} F(W,T,p), \tag{6}$$

which could not be obtained by the balance method that has been used above for T and W. To establish the form of F, a succession model is needed which would operate with the variables m_1 and m_2, which would complicate the development of our model. That is why we assume that during the time $t \sim \tau_p$ when equilibrium is established, $F(W,T,p) \simeq 0$; whence follows an explicit dependence

$$p = f(W,T). \tag{7}$$

This equality is a set of stationary states of p with different values of W and T. Because a reduction of W and T facilities the domination of forest pests, it is true that

$$\partial f / \partial W < 0 \text{ and } \partial f / \partial T < 0 .$$

The function (7) can be very conveniently represented as a set of ecosystem types with ecological factors. In this case, the factors are W and T while the ecosystem types are phases of the exogenetic forest-and-bog succession AF,...,LBC. In the (W,T) plane, these phases take up areas separated by p = const isolines, Figure 4, with p=0 as the baseline.

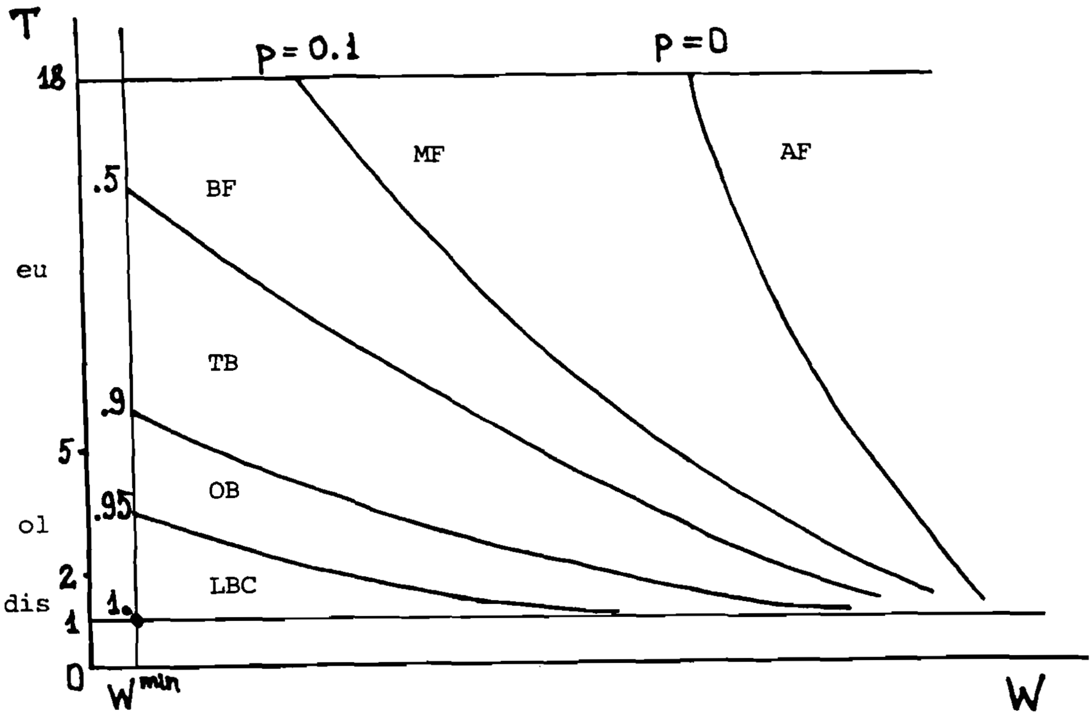

Figure 4: Qualitative ranking of forest-and-bog ecosystem.

Along every isoline, T falls with increasing W or

$$\partial T / \partial W \,|_{p=const} < 0 .$$

In addition, the equilibrium state of FA is naturally assumed to be represented by the p=0 line.

The shape of isolines in extreme conditions such as high aeration with distrophy, low aeration with eutrophy, and low aeration and low trophic content is a separate problem. In Figure 4, these boundaries within which the system exists were assumed to be straight lines, geometrically the simplest possible shape:

$$T = T^{\min} \text{ and } W = W^{\min} ,$$

which is equivalent to the assumption of independent impacts of W and T on vegetation in these extreme conditions. In real life the actions of W and T are not independent and there is, in all probability, no "angle" with $T = T^{\min}$ and $W = W^{\min}$. Besides, the climax state $p=1$ was assumed to be associated only with the point $T = T^{\min}$, $W = W^{\min}$, from which follows that the isolines with $p < 1$, intersect with boundary straight lines. It is indeed possible that there is exactly an isoline p = 1, Figure 5, so that the remaining isolines tend towards it asymptotically. These possibilities need a special discussion in the light of data on the ecology of plants and ecosystems in extreme conditions.

Besides, the sign of the second derivative along the isolines

$$\delta^2 T / \delta^2 W \,|_{p=const}$$

or whether they are convex or concave and whether this derivative changes sign, or whether there are bends, is unknown. Figure 4 assumes concave lines without bends.

4. *$\dot{h}$ as a function of W,T, and p.* Because peat formation occurs in the upper "peat generating" layer with a characteristics Δh of dozens of centimeters, with $h \geq \Delta h$, the growth (or decrease) rate of the peat deposit thickness is in-

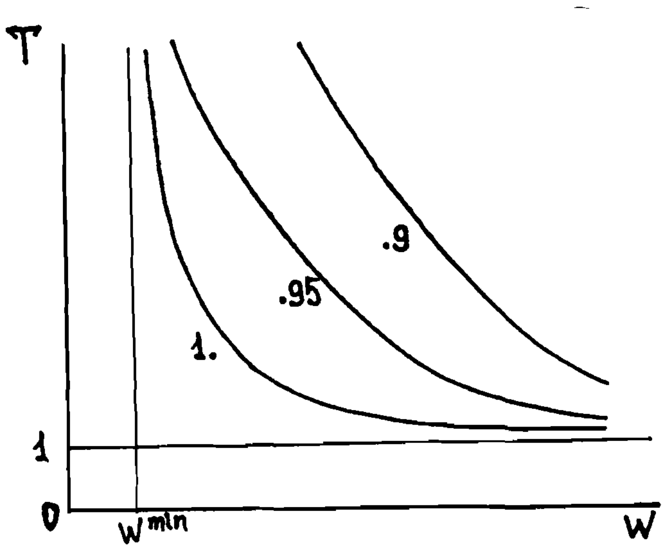

Figure 5: Possible behavior of p=const isolines in extreme conditions.

dependent of h. Let W and T be the aeration of trophic content averaged over the thickness of the grass layer. Let us introduce the rate Q of the inflow of withered phytomass and the specific factors of hygrophyte and tree litter fall, α_g and α_t, respectively. Then, by definition:

$$Q = \alpha_g M_g + \alpha_t m_t = M[\alpha_t + p(\alpha_g - \alpha_t)], \tag{8}$$

where $M = m_g + m_t$ is withered phytomass. In this formula, M and p are functions of the ecological conditions W and T.

As the ecological conditions deteriorate with bogging, or as W and T decrease, the productivity of the location, or M decreases while p(W,T) increases. It follows that the quantity Q given by equation (8) may increase or decrease depending on whether α_g is greater or less than α_t.

The values of α_g and α_t were estimated (P'yavchenko, 1981) using data in the literature on biological productivity of forest-bog ecosystems, see Table 2. The magnitudes are given in metric hundredweights/hectare of drained matter. The factors α_i = litterfall i / m_i.

Table 2: Phytomass fractions and litter for various types of bogs for the taiga zone (P'yavchenko, 1981)

m_t	m_g	M	litter fall t	litter fall g	a	α_t	α_g	p
1670	150	1820	29	28	57	.017	.19	.08
1280	80	1360	19	30	49	.023	.37	.06
390	160	550	8	25	33	.065	.16	.29

Despite the natural variation of values of α_g and α_t, $\alpha_{gk} > \alpha_{tk}$ in every case. This confirms the positive feedback of hygrophytes on peat accumulation, which was mentioned earlier. The reduction of M (by a factor of about three) is offset to a significant degree by the increase of the factor in brackets in equation (8) or by the changing litterfall structure as p grows. As a result, when M falls to one third of its value, Q falls by a mere 30 percent.

Because the root systems are distributed along the vertical, Q depends on h,

$$Q = a + b(h - h^{\min}) ,$$

where a is the litterfall on the surface and b is the withering of root systems in a unit of thickness averaged over h. It is obvious that

$$a = \alpha_g K_g M_g + \alpha_t K_t M_t ;$$
$$b = \alpha_g (1-K_g) M_g + \alpha_t (1-K_t) M_t ,$$

where K_g and K_t are the fractions of root systems in the phytomasses M_g and M_t . Because p and M are functions of W and T, we have

$$Q = Q(W,T,h) = a(W,T) + b(W,T)(h - h^{\min}),$$

while

$$\partial Q / \partial W,\ \partial Q / \partial T > 0 .$$

Let us introduce the rate of decomposition* R of the withered phytomass, a rate which depends on three variables, $R = R(W,T,p)$. R increases with aeration, most probably in direct proportion. The trophic content rate facilitates the prosperity of the microflora which causes the organic matter to decompose; consequently, R also grows with T. Besides, R should also be explicitly dependent on the litterfall structure, i.e. of p. Also, R varies with tree species.

The above data suggest that R decreases as p increases because the decomposition of withered residues of hygrophytes is slower than that of trees. Because p increases as W and T decrease, the function

$$R[W,T,p(W,T)]$$

decreases with decreasing W and T, i.e., with both the explicit and the implicit argument, see Figure 6.

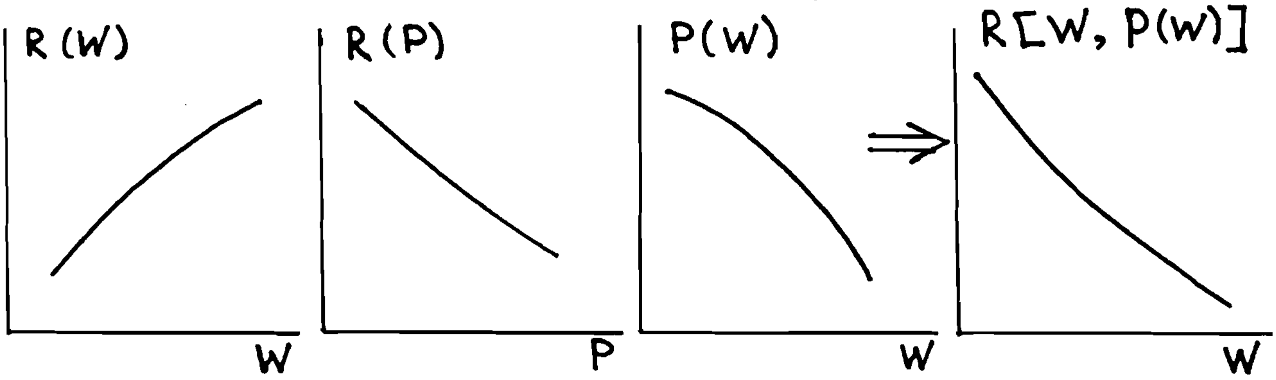

Figure 6: Qualitative dependencies of R on p and W.

Consequently, unlike Q, the arguments W and T "work for the same cause".

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*Q and R are assumed to represent factors which convert a unit of mass m into a unit of layer thickness h.

Assuming that R is the decomposition rate averaged over the entire thickness of the peat-generating layer (Figure 1), two equations describe the dynamics of h before the peat generating horizon has been formed, or for the case of $h \le \Delta h$:

$$\dot{h} = Q(W,T,h) - R(W,T)h \ , \tag{9}$$

and after its formation, or for the case $h > \Delta h$:

$$\dot{h} = Q(W,T,\Delta h) - R(W,T)\Delta h \ , \tag{10}$$

with Δh = const. Let us denote the right-hand side of (10) as

$$\dot{h} = S(W,T,\Delta h) \ .$$

Equations (9) and (10) are key dynamic equations describing the rate of peat accumulation or destruction under various ecological conditions. Together with equations (3), (5) and (7), they make it possible to describe the full dynamics of ecological succession in terms of the above variables.

OPERATION OF THE MODEL: INITIAL BOGGING

With W and T constant, the system finds itself in a state in which the accumulation and decay of the withered phytomass are equal and an equilibrium is reached in (9)

$$h^0 = \frac{a(W,T) - b(W,T)h^{\min}}{R(W,T) - b(W,T)} = \frac{X(W,T)}{Y(W,T)} \ . \tag{11}$$

Equation (10) cannot represent equilibrium and, depending on the sign of $S(W,T,\Delta h)$ either $h \to 0$ or $h \to \infty$.

Equation (9) provides an adequate description of the above sequence of initial bogging with a simple assumption that as aeration decreases, X falls faster than Y and there is a value W = W* at which $h^0 = \Delta h$, Figure 7. Consequently, the value of h^0 in equation (11) increases as W falls, vanishes with W = W* so that with W < W*, it is always true that $\dot{h} > 0$ because once the peat generating layer has formed, W < W* is the domain of infinite peat accumulation.

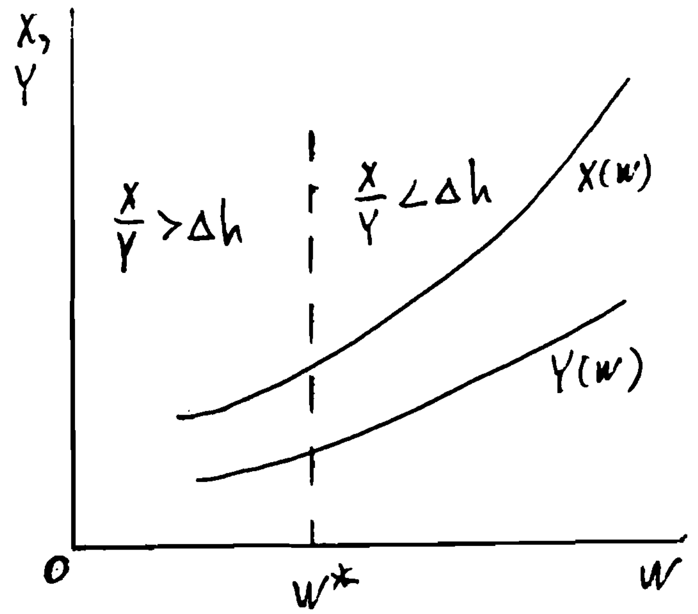

Figure 7: X and Y as functions of W.

The system state with $h \leq \Delta h$ corresponds to the bogged forest, FB, whose basic feature is that the tree roots are in the mineral subsoil. The operation of the model is shown in more detail in Figure 8.

It follows from the above quantitative estimates that

$$\Delta h = \frac{X(W^*,T)}{Y(W^*,T)} = 40cm.$$

In the initial bogging state, the trophic content T of the root layer is relatively constant because T is a function of the amount of mineral matter in the waters and soil that led to bogging and of the trace element content of the tree litter which is constant as long as the tree roots are in the mineral subsoil. It is only in the final stages of peat layer formation in oligotrophic bogging that the trophic content decreases somewhat because of the increased fraction of sphagnum mosses whose trace element content is lower. In this light, at the exogenesis state, T may be

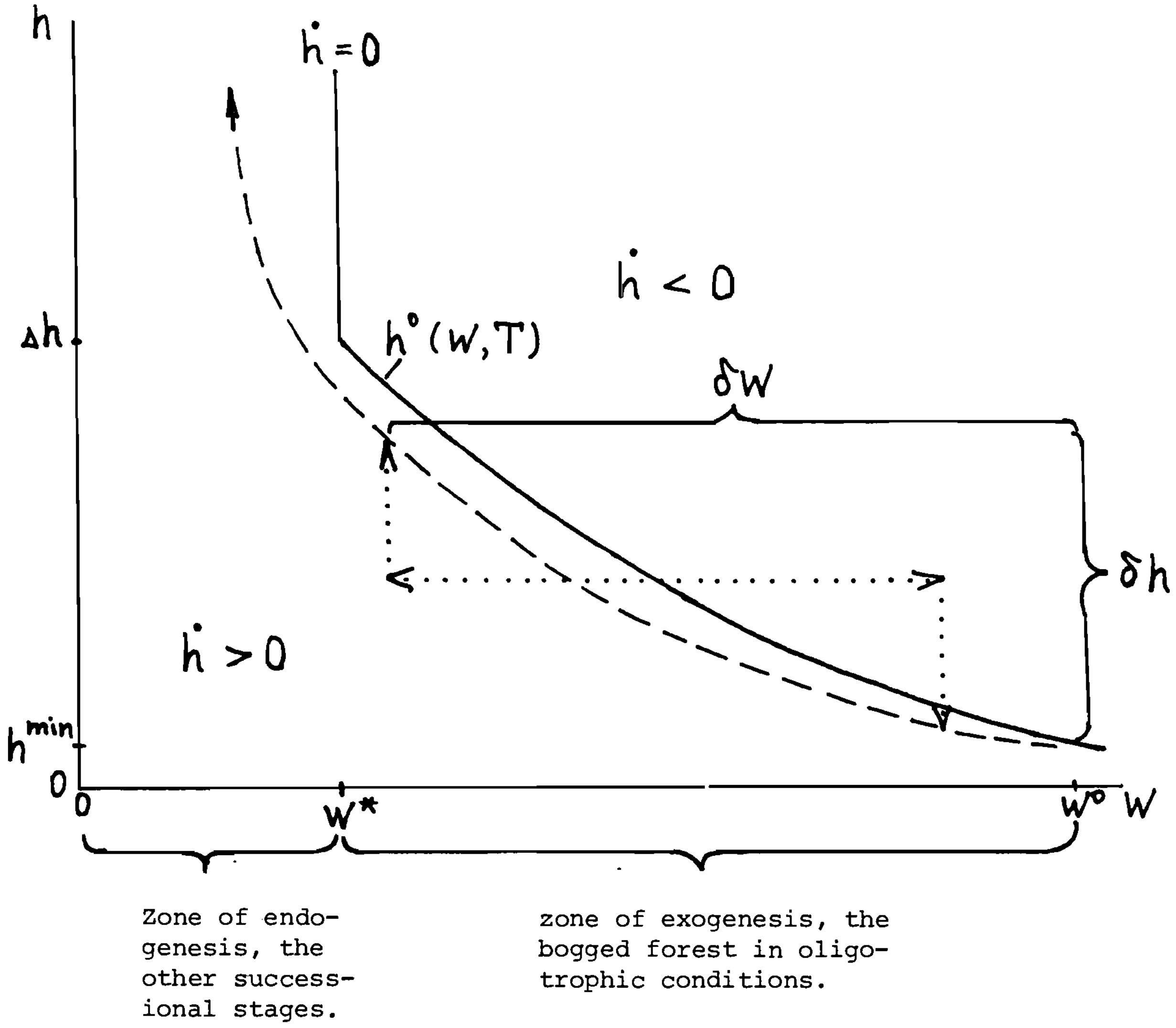

Figure 8: Bogging dynamics in the (W,h) plane in oligotrophic conditions. The $\dot{h} = 0$ curve divides the plane into two parts where $\dot{h} < 0$, $\dot{h} > 0$. δW - the range of aeration with current climatic fluctuations, δh - the associated range of h. The dashed line is the path of values averaged over numerous years by equations (9) and (19). With W , W^* the curve is in the zone of irreversible bogging, or endogenesis. The dotted lines are fast variations of W and h caused by fluctuations around the averages.

viewed as a parameter of the model (9).

In contrast, the aeration W changes to a significant extent. Its fraction drops from the initial to the final stage of peat layer formation. This is attributable to the water-resistant alluvial horizon and the stagnation of water in it.

Generally, a new variable G, the thickness of the gley horizon, has to be introduced in order to describe the dynamics of W(t), also a model of interacting variables W and G has to be developed. In a model of exogenetic succession, this submodel, however, would be only auxiliary. It is described in Appendix II. For simplicity, at this point the function W(t) is assumed given during the entire exogenesis stage.

Let us assume the following scenario for $W(t)$: at time $t = t_0$, W is assumed to change stepwise from W_0 to $W_1 < W_0$, which stands for an exogenous action such as forced watering. If the thickness of the gley horizon remains zero, i.e., G = G (0) = 0, then the value of W also remains constant, W = W_1. However, G starts to cause a reduction in W and this, in turn, facilitates an increase of G. Reasoning in abstract terms, two cases are possible, as confirmed by the submodel of Appendix II.

1. As W decreases, it may stabilize between W* and W, with partial growth of G. A stable bogged forest emerges where the peat generating horizon has not formed.
2. The value of W can reach the boundary value, W*, and decrease below it. G and Δh reach their final values and endogenesis starts. The time within which W = W* is reached is estimated to range from hundreds to a thousand years.

In this sequence, Figure 9, there is a boundary value of the exogenous action W** such that with $W_{1\alpha} > W^{**}$, case α, and with $W_{1B} < W^{**}$, case β is true; with $W_{1c} < W^{*}$, G and Δh reach their final values.

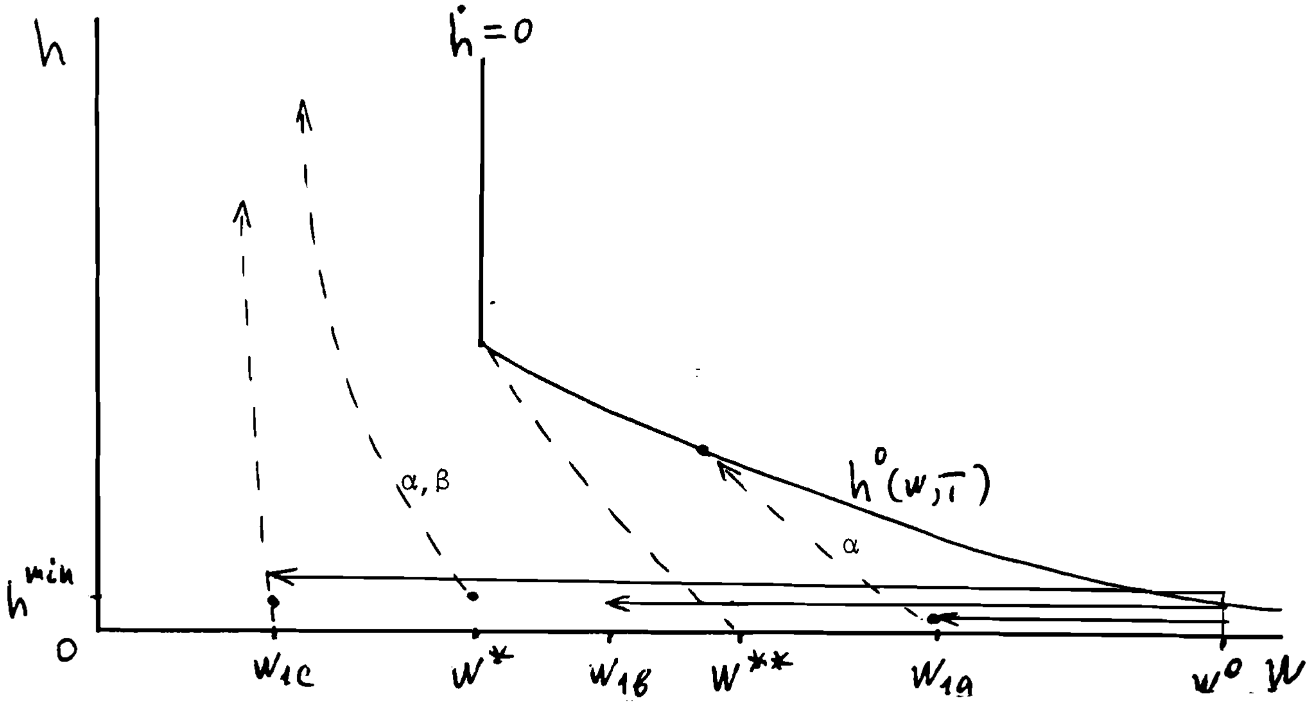

Figure 9: Two cases of bogging with different exogenous forces W_{1a}, W_{1b}, W_{1c} · $\alpha - W_{1a} < W^{**}$, the system stabilizes in the phase of bogged forest with G and Δh underdeveloped. $\beta - W_{1b} > W^{**}$, the system changes to the endogenesis phase. Solid arrows denote the initial stepwise change of W and the dotted arrows, subsequent slow evolution.

In this bogging mechanism there are two different characteristic times in the system (see also Figure 8). Fast movement (dotted line in Figure 8) occurs when the fluctuations in phytomass withering attributable to the fluctuations of W and climatic parameters push the value h away from the quasistationary value h^0. Within several years, the excessive litter decomposes and the shortage of litter is replenished. In fact, because of continual fluctuations the path hatches a strip around the curve $h^0(W,T)$; the W dimension of the strip is equal to the characteristic amplitude of aeration and the h dimension, to the water level. The other, slow movement, is attributable to the alluvial horizon and slow reduction of the average value of W. The path of slow movement obtained by averaging over δW, δh is somewhat below curve (II).

Model behavior with different values of T follows from the reasoning in an earlier section. Because a higher trophic content favors the domination of trees which inhibit peat formation, with higher trophicity, lower aeration is necessary for the system to reach the zone of infinite peat accumulation. Consequently, $W^*(T)$ is a diminishing function of T, Figure 10a.

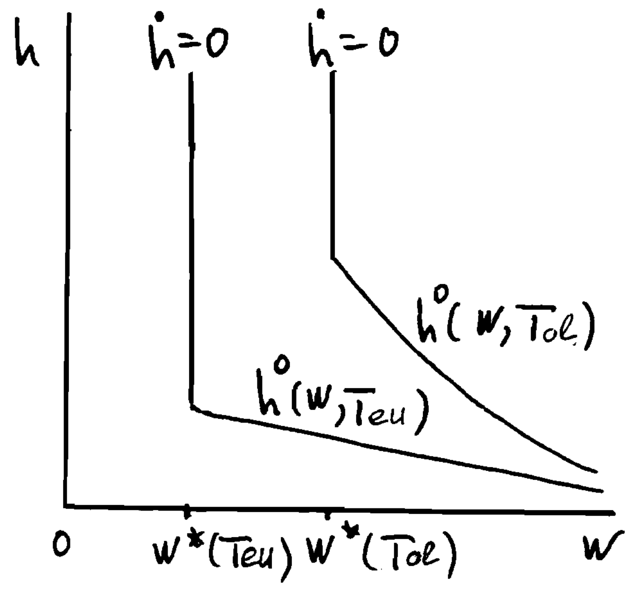

Figure 10a: Change in the position of the $\dot{h} = 0$ curve, Figure 8 with trophic content variation.

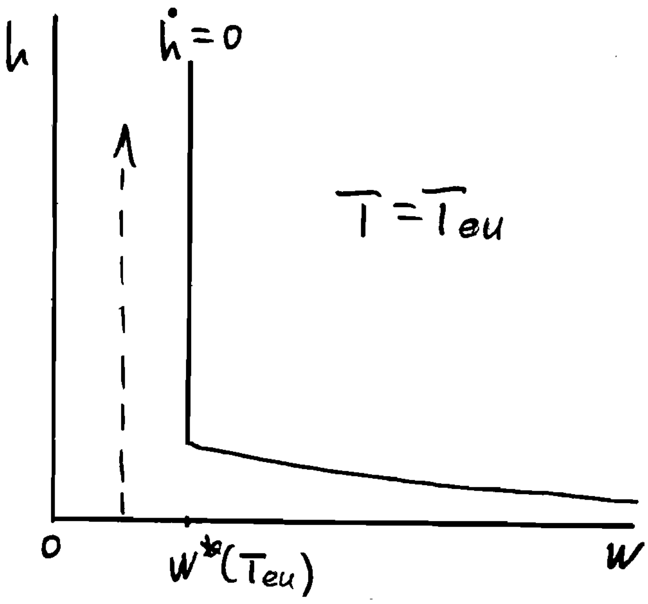

Figure 10b: The case of high water table, the endogenous stage is skippled.

The case of eutrophic bogging is interpreted in the model in the following way. The exogenous action which specifies the value $W_{1d} < W^*$, Figure 10b, results in a strong water head which inhibits the development of a gleyic horizon. The bogging remains exogenous.

OPERATION OF THE MODEL; COMPLETE EXOGENESIS CYCLE

Once the initial bogging has been described, we can supplement Figure 4 with a boundary curve W*(T) which separates the exo- and endogenesis zones. In the model development sequence, W* is the Δh -averaged aeration value with which

$$R^{\min} + R(h - \Delta h, T) = 0$$

where $\Delta h = \bar{\delta}a$ is the variation amplitude of the water level averaged over many years. Values of W* can be found from the basic dynamic equation (9) bearing in mind that these values are associated with the maximal value of $h^0 = \overline{\delta a}$:

$$Q(W^*, T, \overline{\delta a}) - R(W^*, T)\, \overline{\delta a} = 0 \Longrightarrow W^*(T, \bar{\delta}a) . \tag{12}$$

Because the zone of initial exogenesis is ecologically associated with BF, the W* (T) line coincides with the isoline p = .1 (denoted as Γ below).

Model behavior with $W < W^*$ is shown in Figures 11-14; Figure 11 is represents a forest-and-bog ecosystem supplemented with a boundary curve W*(T) and the paths of variables of Figures 13 and 14. Figure 12 shows the growth rate

$$\dot{h} = S(W, T, \Delta h) \tag{13}$$

as a function of W and T. In extreme ecological conditions near the boundary of existence of vegetation, with $W = W^{\min}$ and $T = T^{\min}$, the rates of phytomass inflow Q and decay R are nearly 0 so that

$$S(W^{\min}, T^{\min}, \Delta h) = 0 .$$

Besides, with W and T assumed to be given parameters, we have $\dot{h} = 0$ and in the entire initial endogenesis zone, $0 \leq p < .1$.

Possible dependence of S on W and T in Figure 12 is recognized in the arguments of the function S.

By varying initial conditions and the form of the function T = m(h) and W = g(h) and recognizing the exogenous action, model (13) makes it possible to

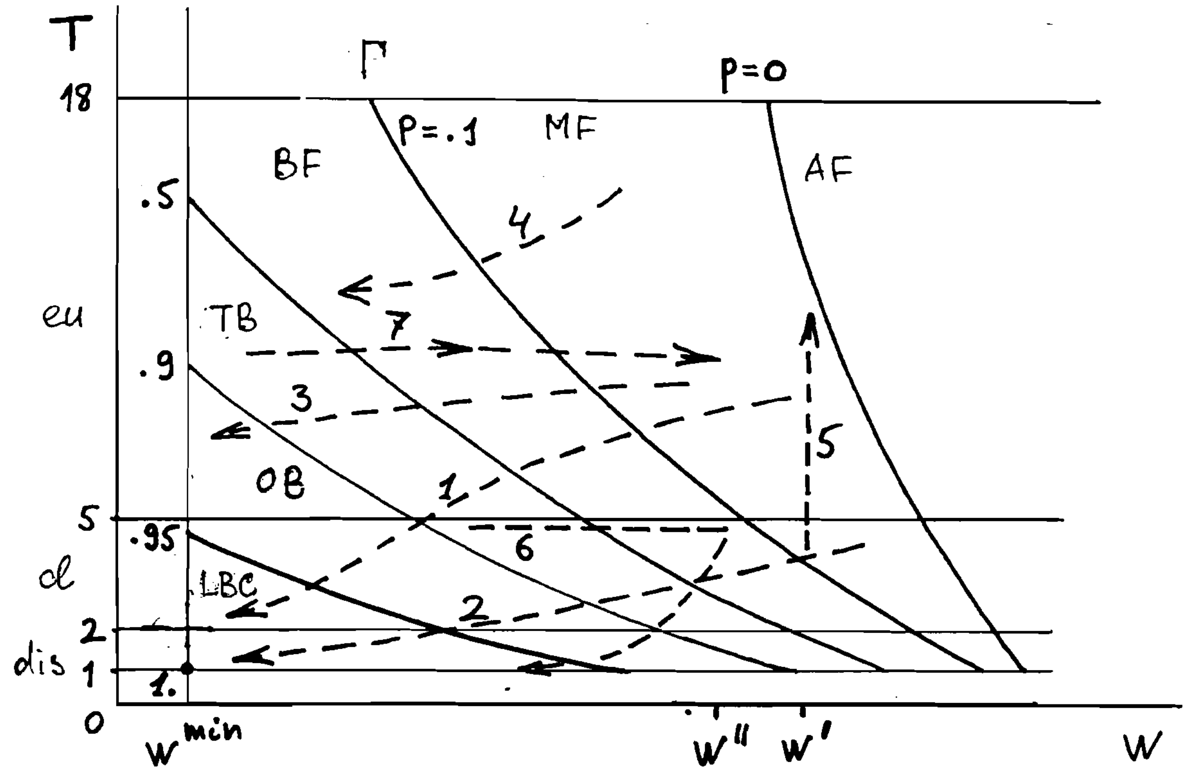

Figure 11: The ordinate plane for an exogenetic succession with curve Γ superimposed. 1 - 7 are paths of W as a function of T in various conditions (see text and Figures 13 and 14).

describe the kinds of forest-bog alterations observed during exogenetic succession (Glebov, 1984).

These alterations are triggered by combinations of three elementary dynamic processes

a. Forest-and-bog peat accumulating endogenesis, for brevity endogenesis hereafter, whereby p and h increase;

b. Bog-and-forest peat-destroying exogenesis (referred to hereafter as exogenesis; the term also covers the initial exogenesis of the preceding section) whereby p and h decrease.

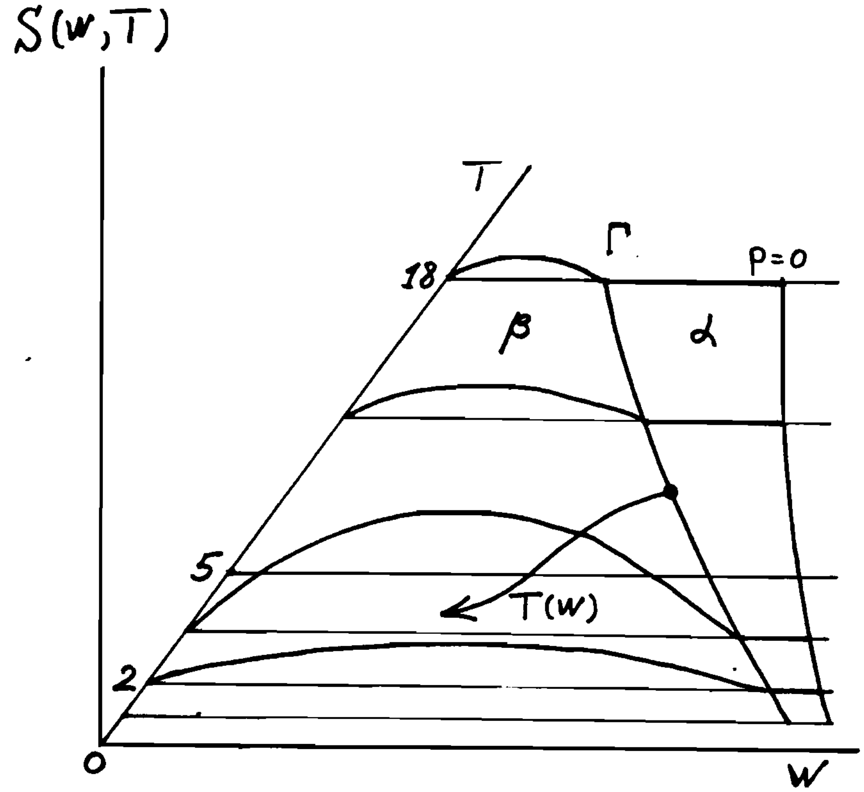

Figure 12: Qualitative pattern of peat accumulation rate as a function of W and T. Γ - the W*(T) curve separating the exo- (α) and endogenesis (β) zones. T (W) - the path of a specific system.

c. Bog-and-forest peat accumulation exoendogenesis (hereafter referred to as exoendogenesis whereby p decreases and h increases).

Let us consider the dynamics of variables in these three cases.

A. Endogenesis dynamics. The chief component of this process is the ecological evolution from MF (following the initial exogenesis of the preceding submodel) to LBC and peat accumulation. Early in the bogging processes, conditions are somehow created for excessive aeration and peat accumulation as an outcome of accumulation of unconfined ground waters in terrain depressions, water resistant horizons resulting from permafrost when the climate gets colder (which in all probability is what happened in the second half of the pre-boreal period), tectonic elevation of the earth's surface or lowering of the surface due to river erosion.

Once the peat-generating horizon has formed, the process continues, zone β in Figure 12.

In all cases, hygrophytes become embedded, accelerating the growth rate of p (the maximum rate being in the FB and TB phases) and of h; and decreasing W and T. These variables stabilize in the climax state of LBC when and if this forms.

For an average case (curve I in Figures 11 and 13), each phase is assumed to take approximately the same length of time and all three trophic content grades, eu-, oligo, and dys- are assumed to occur in succession. The typical time for the entire sequence of phases MF, BF ... LBC is 5,000 to 9,000 years, the average rate of h growth being about .5 - 1.mm/year.

In harsher northern conditions with a reduced initial trophic content, the evolution time is reduced and through the bog phases, extended; the case being reversed in the south with higher trophic content. In extreme oligotrophic conditions, in particular when the bogging starts in impoverished outwashed sands, the eutrophic stage is skipped and the bog phases proceed at the slowest possible rate, path 2 in Figures 11 and 13. The oligotrophic phase is skipped in eutrophic conditions with a head of ground or meadow water. In this case, the trophic content does not change much in the development process. As a result, LBC cannot form and the process terminates in the OB phase, path 3, Figures 11 and 13. With W and T especially high, the bogging process cannot go beyond the primary FM stage, path 4, Figures 11 and 13.

Figures 13 and 14 do not show the dynamics of soil aeration because at this stage of bog research, no tools are available for retrospective measurement.

B. Exogenesis dynamics. This process is the opposite of the preceding one and amounts to evolution from any forest-and-bog phase, to destruction of the peat by oxidization of the organic matter and erosion during which p and h diminish while W and T increase. This process, which cannot start until peat has accumulat-

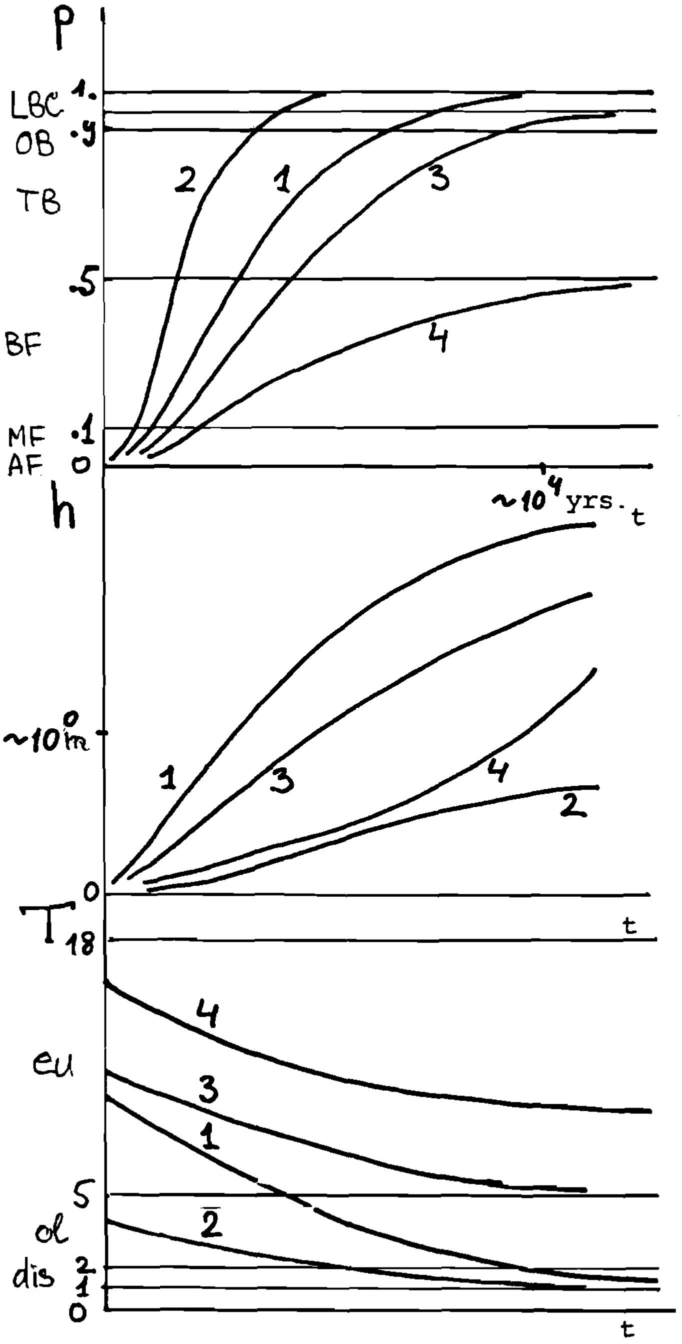

Figure 13 The endogenesis dynamics of the forest-and-bog system with different water supply conditions. 1 - standard case when all stages of trophic content evolution occur; 2 - bogging in oligotrophic condition; 3 - in eutrophic conditions; 4 - with a strong head. The associated paths in the state plane (W,T) are shown in Figure 11.

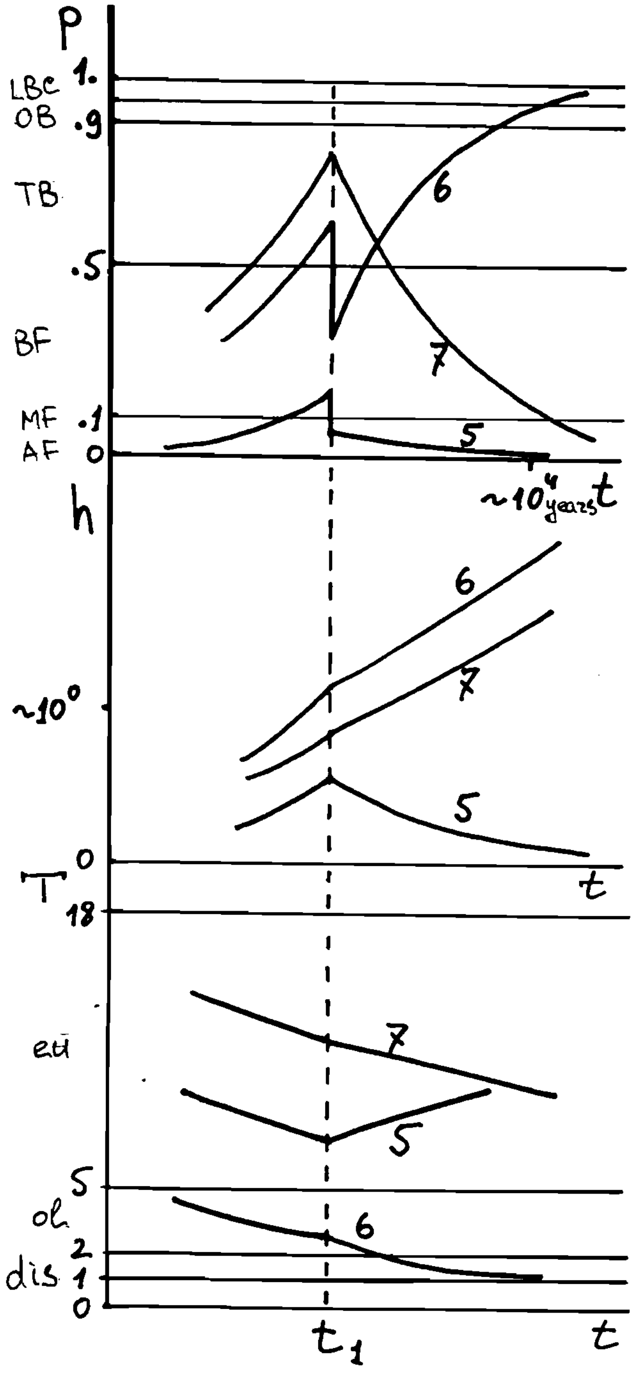

Figure 14: Endogenesis halted at time t_1 by drainage which increases the value of aeration W. 5 - endogenesis with destruction of the peat deposit and growth of a stable automorphous forest AF (the case of W abruptly changing to W' , Figure 11); 6 - endogenesis in oligotrophic conditions with continued peat accumulation, short-lived reaforrestation and rebogging (the case of W abruptly changing to W" with subsequent endogenesis, Figure 11); 7 - exoendogenesis in eutrophic conditions with stable afforestation (the case of slow growth of W).

ed (as a result of endo- or exogenogenesis), is caused by exogenic causes leading to drainage of the bog. This may be natural drainage by climatic drying, lower base line of erosion, upward tectonic movements, or man-made drainage.

In the model, exogenesis maintains the system in the BF domain, left of the Γ line, Figure 11. This may occur by changing W through natural drainage or by land development.

In the north and in oligotrophic conditions, exogenesis is not observed today except in cases of man-made drainage. In the past, however, this was a widespread phenomenon which is evidenced by the climatically induced (by warming) so-called boundary peat horizons and the stumps buried in them; these large trees no longer grow in high moors.

In the south and in eutrophic conditions where the forest is more stable, this process is fairly widespread, particularly in the southern taiga subzone of Western Siberia. Here it is triggered by positive tectonic movements (Orlov, 1968) and, possibly, by the currently unstably humid and continental climate which does not favor bogging (Glebov, 1977). An example of bog afforestation and peat deposit degradation as a result of drainage is shown as path 5 in Figures 11 and 14. Other kinds of dynamics are, of course, possible.

C. Exoendogenesis dynamics. This process is a cross between the preceding two and cannot start unless drainage favors the growth of a forest but is not so strong, as in the case of exogenesis, that it prevents peat accumulation.

In our model, the process is described in the following way, As in exogenesis, the variable W is "forcibly" increased but remains to the left of curve Γ , or in the peat accumulation domain. The increase of W results in afforestation which is, however, unstable because of the continuing peat accumulation ($\dot{h} > 0$) leading to a fall of T.

In the oligotrophic phase, the emerging forests are unstable for the following reason; if the cause of maintaining W is removed, exoendogenesis is replaced by "pure" endogenesis and the forest is replaced by a secondary bog. Such short-lived forests are, in particular, those on the slopes of convex bog areas; the trees die when the bog surface becomes more level,, which hinders drainage and reduces W. This case is shown as path 6 in Figures 11 and 14.

If exoendogenesis occurs at the eutrophic stage (with a high water table or alluvial water supply), the secondary forests are very stable and spread more widely than those which result from exogenesis. In particular, they now take up vast areas in Western Siberia. An example of this kind of dynamics is shown as path 7 in Figures 11 and 14; in this case, exoendogenesis took over from endogenesis at the TB phase leading to FB.

If W is artificially maintained at a given level, which is typical of the southern taiga subzone, then the ecosystem achieves a pseudoclimax. If W is subjected to a single short-lived impact, rebogging occurs very quickly fast with low trophic content.

In concluding the discussion of the dynamics of variables which describe the elementary forest - bog alternations, the basis evolution path is a repeated replacement of endogenesis by exoendogenesis and exogenesis so that the evolution of a specific forest-and-bog ecosystem may be extremely complicated because such systems are labile to a certain extent, depending on the development of the entire moorland, and on the intensity of exogenous factors.

DISCUSSION

A. The proposed model is the simplest possible approximate description of a vertically distributed system such as a peat land, viz a two-point approximation in which the vertical profile is divided into two parts, the peat-generating layer and peat, if this exists. Because our goal was to obtain an ecologically sound description of the initial phase and subsequent exogenetic succession, we did not try to formulate a rigorous (continuous) vertically distributed model at the first stage - there were no data for applying the model to a specific location and this dictated the choice of the two-point approach for describing the qualitative properties of the process.

B. By their generality, the functions (3), (5), (7) and (9) are classified into two groups. One includes:

$$T(h) \text{ and } W(h)\ , \tag{14}$$

which are "individual" in that they describe the water supply, terrain, etc., of a specific location and also include the water level variation range $\overline{\delta a}$ which dictate Δh. The other group includes:

$$Q(W,T), R(W,T) \text{ and } f(W,T)\ , \tag{15}$$

which are "general" in the framework of the initial assumptions and are supposed to be applicable to all forest-and-bog systems in a climatically uniform area. For a specific area, these functions should be determined as a first priority. For the functions (14), the typical dependencies averaged over the area are needed.

C. Our concepts of endo- and exogenesis are two idealized extreme cases of the actual situation which must be very complicated. For long-lived exogenesis (debogging), high aeration has to be maintained artificially. If, however, highly productive secondary marshy forests have grown whose taxational indicators are nearly those of the automorphic forest, the tree stand transpiration becomes so powerful that there is no need to maintain high aeration exogenously. Antonovsky et al (1980) have proposed a possible model description of this effect. Once this state has been achieved, peat destruction proceeds by itself. At this stage the exogenesis is in fact replaced by endogenesis which is peat destructive rather than peat accumulative. Consequently, there is no essential difference at this stage between exo- and endogenesis. A similar situation is observed in initial endogenesis (see Figure 9 where the exogenous action reduces W and results simultaneously in formation of a impermeable horizon).

D. The model predicts events which are not represented in the initial data but seem to occur in real life, e.g., a peat-destroying tree stand resulting from extensive drainage which increases W. Examples of peat deposit debogging by a forest in various situations have been provided elsewhere (Glebov, 1986).

APPENDIX I: A qualitative model of bog-lake alternations

For illustration, a qualitative model of bog and lake alternations will be briefly described.

A lake, as well as a forest, is a widely known initial state for bog formation, in this case through lake-bog succession.

In terms of accumulation and decay of the withered organic matter, a stably existing lake is quite similar to an automorphic forest in that it is a system in which the withered organic matter decays completely. What is different is the dependence of this balance on W and T: as in the case of forest, an increase of W serves to preserve the lake but an increase of T results in bog-favoring eutrophication. Consequently, the boundary curve φ which separates the lake from the bog on the (W,T) plane has a slope opposite to that of the curve Γ which separates the forest and the bog, Figures A1.1 and A1.2. In this case W and T oppose rather than support one another.

To interpret these two states in the same light, a variable should be found which distinguishes between them. Such a natural variable is the amount of water (precipitation, humidity), A, in a unit system volume (in soil for the forest, in the peat generating layer for the bog; in the lake, this unit makes sense, bearing in

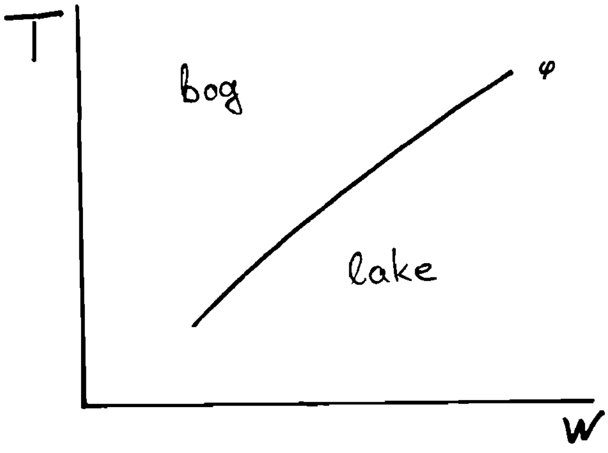

Figure A1.1:

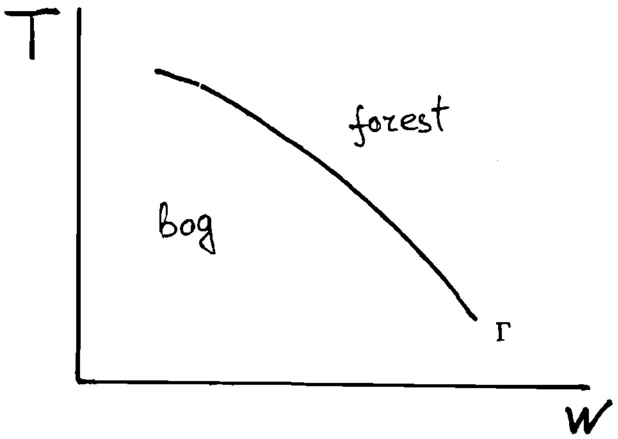

Figure A1.2:

mind the amount of organic matter). On the (W,A) plane, the three systems are arranged in increasing order of moisture from the automorphic forest to clear water, Figure A1.3.

In Figure A1.3 the top area is probably the steppe where the decay rate is limited by shortage of water.

A picture in which all three ecological factors are represented is given in Figure A1.4. To avoid complicating the final picture with a structure in the three-dimensional space (W,T,A), only the variation of the two-dimensional mapping of Figure A1.3 with trophic content variation (increase) is shown in Figure A1.4.

This approach may result undoubtedly in a fully-fledged model which would be as sound as the above exogenesis (forest-bog) model.

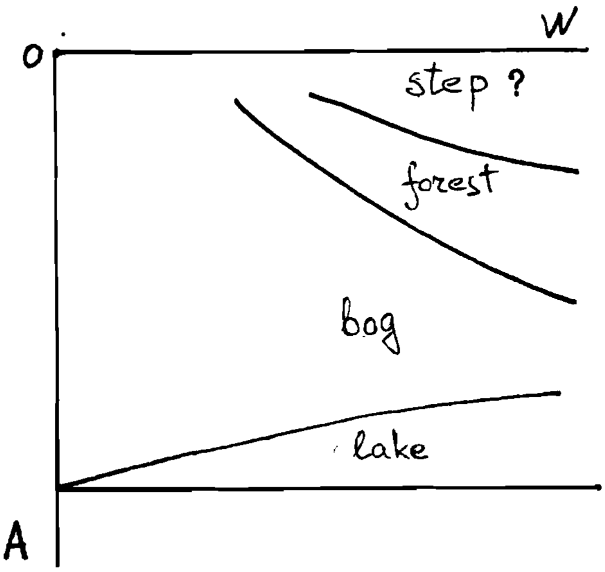

Figure A1.3: The plane of ranking in terms of variables W and watering A for three types of ecosystems. The slopes of dividing lines represent the impact of the ecological factors introduced into the model on the possibility for these types to exist.

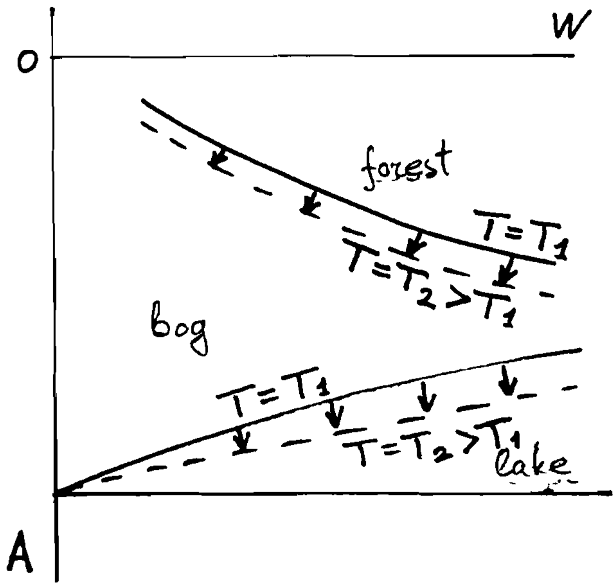

Figure A1.4: Shift of boundaries between three types of ecosystems with trophic content changes.

APPENDIX II.

Let us consider a straightforward model representing the simultaneous dynamics of aeration W and the thickness G of the alluvial (gleyic) horizon with excessive watering, a model which may supplement the basic model forest-bog dynamics.

A. Assume that:

- the function U(t) is the rate of oxygen accumulation in the soil water. This inflow of O_2 is made possible by exogenous factors such as mixing due to a change of the water table and head and the rate of water inflow and rain (snow) fall;
- the function C(G) is the mixing factor (reverse of stagnation) which depends on the possibility of infiltrating the ground as well as on exogenous causes and is dictated by the thickness G of the gleyic horizon. The maximal mixing with

G=0 is equal to 1 and falls monotonically as G increases, Figure A2.1;

- the function a(w) is the rate at which oxides which make the gleyic horizon are accumulated in the soil; this function obviously grows with W, Figure A2.2;
- The function b(w) is the specific rate at which these oxides oxidize to eliminate G; this rate obviously grows with G, Figure A2.2.

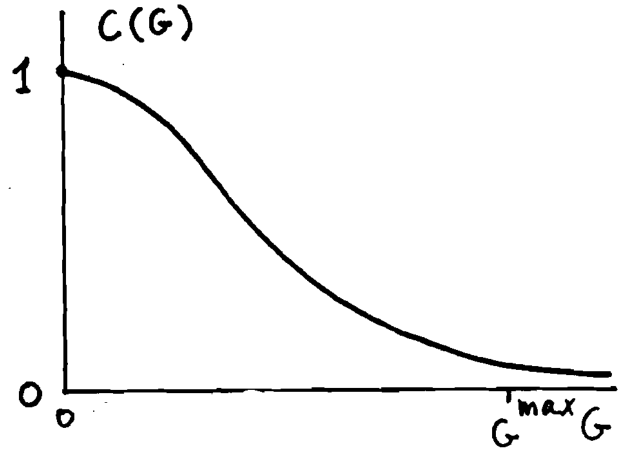

Figure A2.1: Qualitative mixing factor (C(G) responsible for the specific rate of growth W.

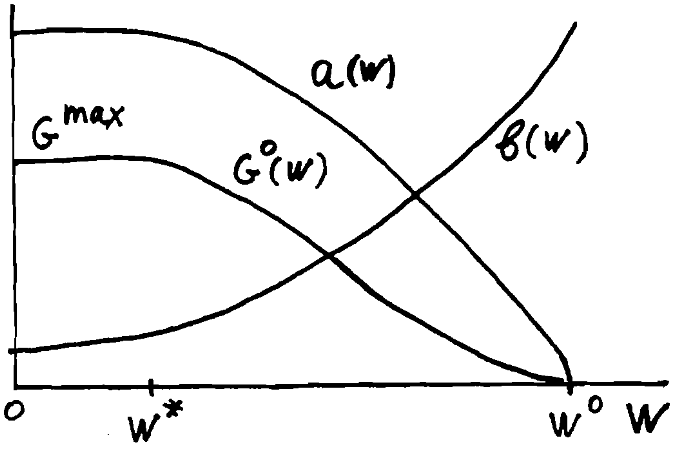

Figure A2.2: Qualitative function a(w), of formation and b(w) specific destruction rate of oxide compounds; $g^0(w)$ - equilibrium values of G with a fixed $W.W_0$ - maximal (inititial) value of aeration.

It would be a natural assumption that, up to the recession, G is a monotonic function of W reaching a maximum at some fairly low value $W=W^{min}$. From the reasoning used in developing the basic models, Equations (9) and (10) and Figure 8, it follows that W^{min} can be assumed equal to W*, or the value of W at which the process reaches the irreversible stage of bogging. Consequently,

$$G^{max} \simeq a(W^*)/b(W^*);$$

Assume also that $G(W<W*) = G^{\max}$, Figure A2.2.

In terms of the quantities introduced above, the equations for the dynamics of W and G are

$$\dot{w} = [U(t) - \frac{1}{C(G)}W]\frac{1}{\tau_w}; \qquad \text{(A2.1)}$$
$$\dot{G} = [a(w) - b(w)G]\frac{1}{\tau_G},$$

where the factors are identified equal to inverse characteristic times of gleyic horizon formation (τ_G) and adjustment to hydrologic conditions (τ_w). Empirical observations reveal that $\tau_G \sim 10^2$–10^3 years, $\tau_w \sim 10^{-1}$ years, or $\tau_w << \tau_G$.

The set of equations which define the possible equilibrium values of the system (2.1) in a stationary environment, or with $\mathrm{T}(t) = \text{const}$

$$UC(G) - w = 0$$
$$a(w) - b(w)G = 0 ,$$

is reducible to the equation

$$W = UC[\frac{a(w)}{b(w)}] \qquad \text{(2.2)}$$

or

$$w = UZ(w) .$$

Depending on the form of the function z(w), this equation may have one or three roots, one and only one root in the case of a convex function z'' (w) > 0, Figure A2.3; one or three roots with a concave function z''(w) < 0, Figure A2.4.

B. The model operation is shown in Figures A2.5 and A2.6.

Let us assume that the function z(w) is convex, Figure A2.3, $G = 0, C(\vartheta) = 1$, and, with high $W = W_0$ $a(w_0) \simeq 0$. In this situation, the value of w(t) adjusts quickly to the current value of aeration U(t), specified exogenously, or

$$W(t) \simeq U(t)$$

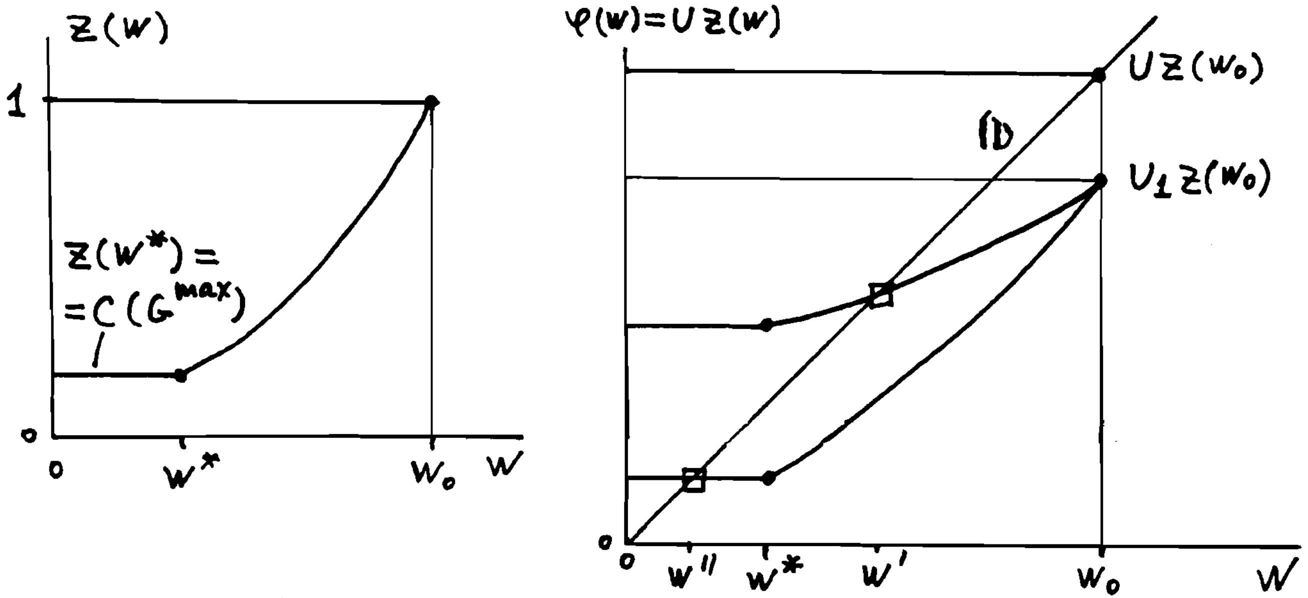

Figure A2.3: Convex $z(w)$ line yields one root of equation (2.2) with any value of exogenously specified aeration $U_1 < w_0$. This root is on the right of (w') or left of (w") the boundary values of W*. The root value grows with T as a parameter for the specified function z(w). Straight line γ is a diagonal.

with an average value

$$\overline{U(t)} = W_0$$

while it remains true that $G(t) = 0$.

Assume also that at time $t = t_1$, the exogenously specified aeration changes stepwise in response to an increase or another abrupt change in hydrological conditions so that $U(t) = U_1$. Initially W falls quickly to $W = U_1$ while $G(U_1) = 0$ and a(w) and b(w) change stepwise

$$a = a(U_1) \text{ and } b = b(U_1).$$

The characteristic time of these changes is τ_w.

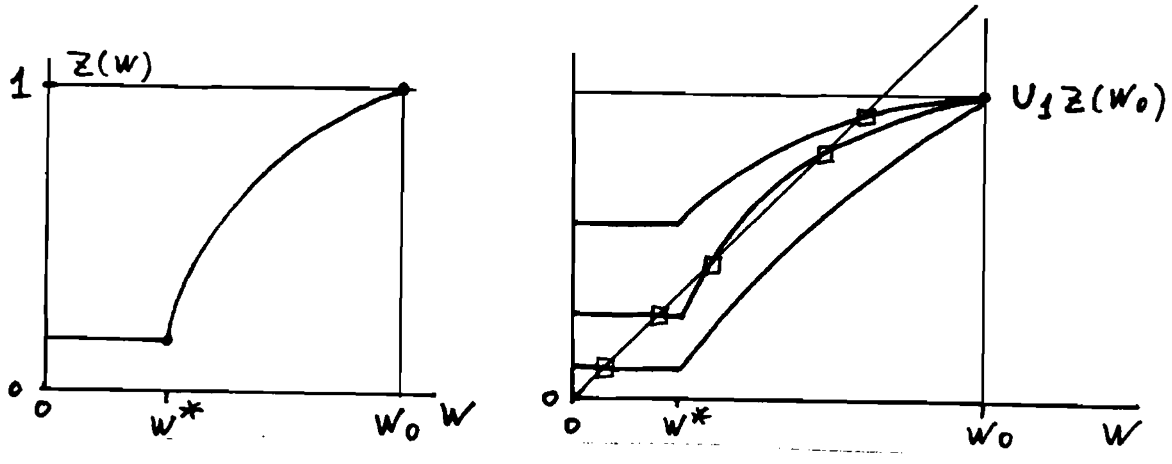

Figure A2.4: The concave function z(w) yields one or three roots of the function (2.2).

Then G slowly increases with a $(U_1) > 0$ so that the entire system changes, the characteristic time being τ_G .

In terms of the bogging dynamics in the basic model, the critical value of W is W*; Figure 2.3 demonstrates that there is a boundary value of the exogenous $U_1 = U_1^{\bullet}$ such that with $U_1 > U_1^{\bullet}$ the system stabilizes in a state for which $W' > W^*$ and $G' < G^{\max}$, Figure A2.5. This is the case of incomplete bogging with stabilization in the phase of bogged forest, BF, Figure 9.

When $U_1 < U_1^{\bullet}$ is strong enough, there is an equilibrium at W" < W*; the process reaches a boundary value of W* and the maximal gleyic horizon $G^{\max}$ forms. The system moves into the domain of irreversible bogging with W gradually diminishing. See Figure A2.6.

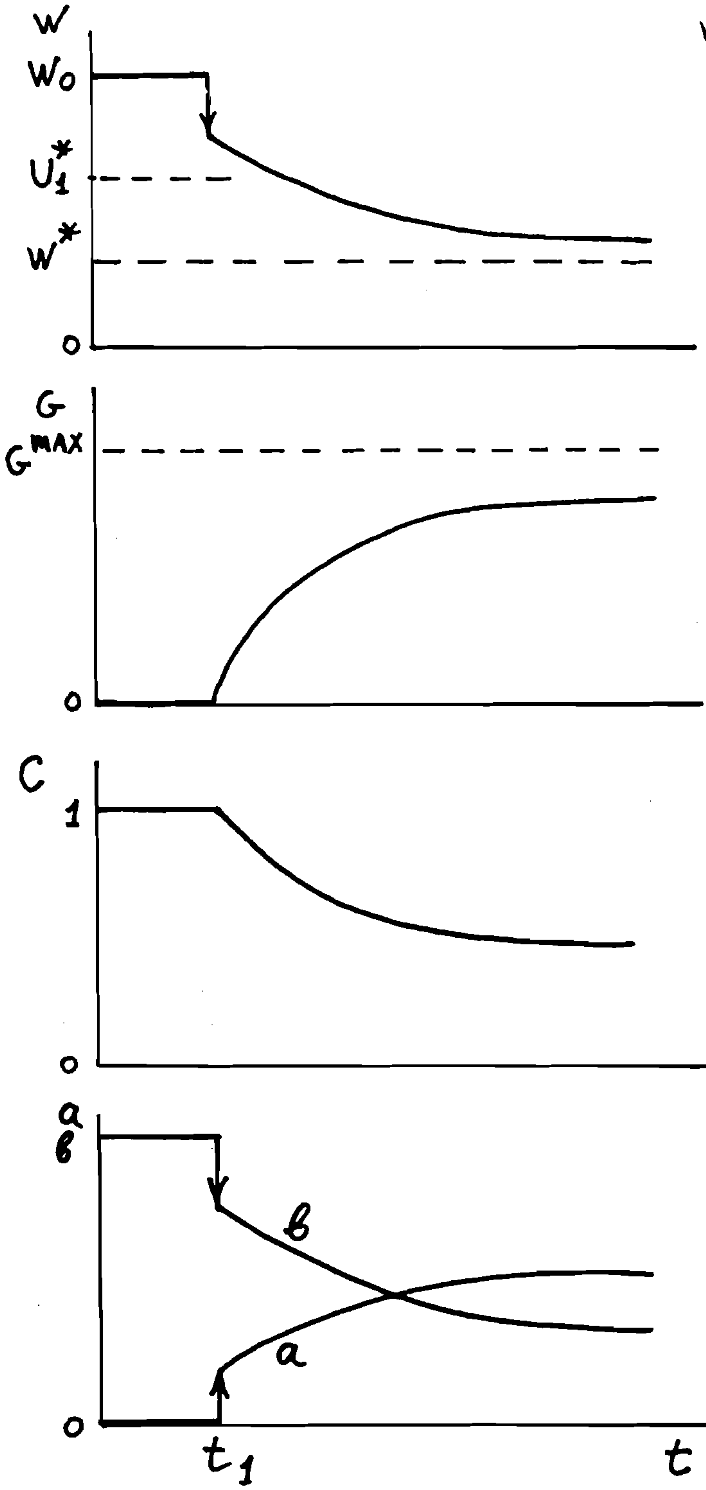

Figure A2.5: Dynamics of variables of the set (2.1) with stepwise change of aeration $U_1 > U_1^*$ (at time t_1).

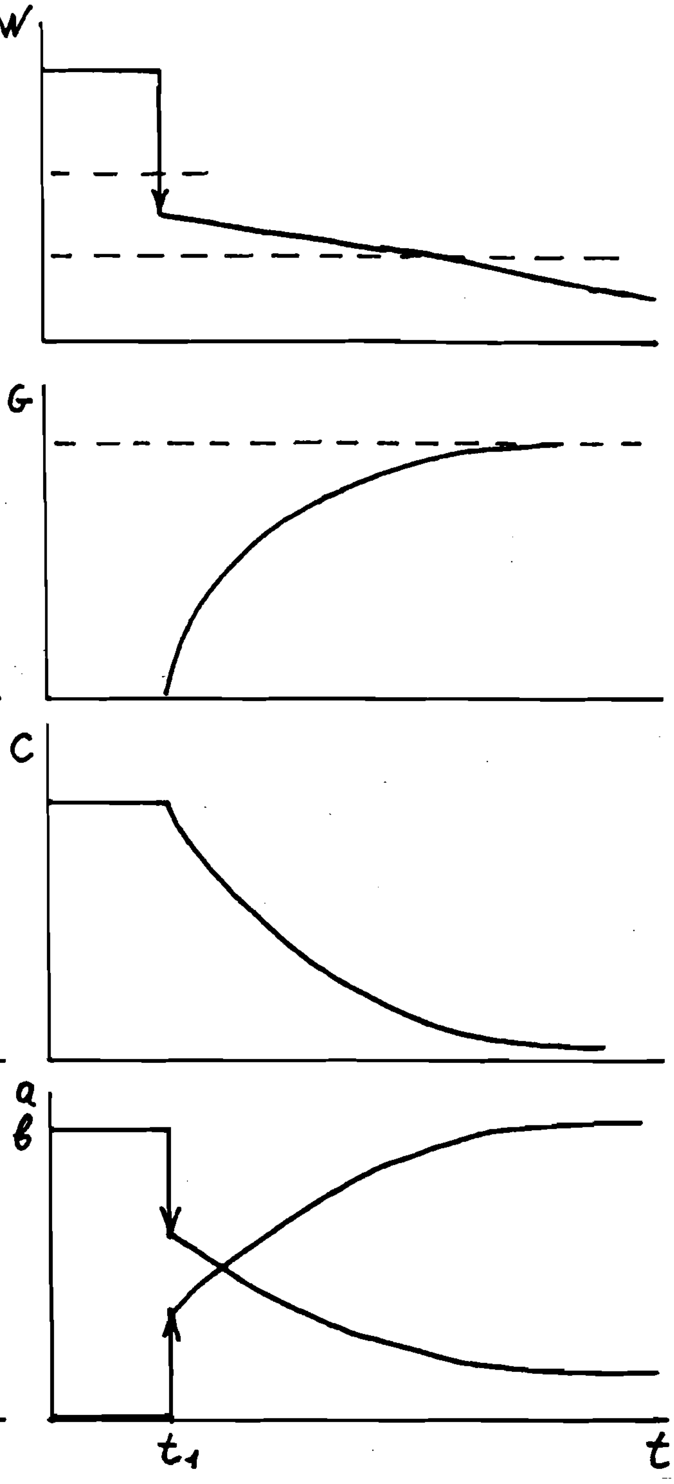

Figure.A2.6: Dynamics of variables of the set (A2.1) with stepwise change of aeration $U_1 < U_1^*$ (at time t_1).

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