WORKING PAPER

THE DYNAMICS OF FOREST DECLINE

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FOREWORD

Within IIASA's Environment Program, the Biosphere Dynamics Project seeks to clarify the policy implications of long-term, large-scale interactions between the world's economy and its environment. The project conducts its work through a variety of basic research efforts and applied case studies. One such case study, the Forest Study, has been underway since March 1986, and focuses on the forest-decline problem in Europe. Objectives of the Forest Study are:

(a) to gain an objective view of the future development of forest decline attributed to air pollution and of the effects of this decline on the forest sector, international trade, and society in general;

(b) to build a number of alternative and consistent scenarios about the future decline and its effects; and

(c) to identify meaningful policy options, including institutional, technological and research/monitoring responses, that should be pursued to deal with these effects.

This paper outlines a theoretical framework for understanding forest decline attributed to air pollutants. Finnish examples are used to demonstrate applications of the approach.

B.R. Döös
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SUMMARY

The anthropogenic emissions into the atmosphere have changed the material flows in the system formed by the atmosphere, vegetation, soil, groundwater, and surface waters. The concentrations of several nutrients and toxic compounds are changing. These concentrations are environmental factors and forests are reacting to the changes in the environment.

The material flows are analyzed and basic structures to describe the changing concentrations are outlined. Soil acidification is used as an example of changing environmental factors. The photosynthetic and nutritional response of trees is modeled. Aggregated variables are introduced to describe annual effects of environmental change on metabolism of trees. A stand growth model is described in a static environment and necessary modifications in a changing environment are introduced. A more aggregated model to account for the effects of changing environmental factors on forest growth is described.

CONTENTS

THE DYNAMICS OF FOREST DECLINE

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1. INTRODUCTION

This paper outlines a theoretical framework for the analysis of forest decline. The framework links the functioning of a forest stand with environmental factors, thus enabling the stand's response to changing environmental factors to be predicted. The framework, which is expressed in the form of a hierarchical family of dynamic models, is demonstrated by examples from Finland.

Plants respond primarily to their microenvironment, i.e., the properties of the immediately surrounding atmosphere and soil. The microenvironment is a part of the local environment of the stand, which in turn interacts with the larger environment of the region. This division into micro-, local and regional environment is artificial, but serves to stress that the temporal features of the environment are associated with the spatial features. The temporal scale of the microenvironment is in the range of seconds to days, that of the local environment of hours to years, whereas the regional environment changes over years to centuries. The dissipation of energy in the atmosphere of the earth follows the same pattern; large-scale motion is much more predictable than the final dissipation due to small-scale turbulence. Air dispersion modeling is one reflection of this phenomenom.

The paper is divided into five chapters. Chapter 2 describes the environmental characteristics that we consider important for forest growth. Special emphasis is given to a quantitative definition of the environmental factors and to a method for analyzing their dynamics. A strong relationship exists between the immediate state of the environment and the functioning of trees. A forest stand forms a functional unit which is normally characterized by an area of several hectares and a time span of about a century.

A forest region comprises stands of different age, type, structure, etc., and may extend to hundreds of hectares. The use of knowledge about plant function in the analysis of stand development and regional forest growth forms a methodological problem of aggregation or scaling-up. Chapter 3 considers the stand development. The focus is on functionally based aggregation of environmental factors and on the use of stand models. The question of aggregation is also addressed in Chapter 3. Chapter 4 enlarges the scope to the regional level. The paper is closed with concluding remarks in Chapter 5. The report is a direct continuation of our previous work reported by Raunemaa et al. (1982, 1987) and Hari et al. (1986, 1987).

2. ENVIRONMENTAL FACTORS

2.1. General

Environmental factors are the properties of the environment that influence the metabolic processes of plants and include irradiance, temperature and concentrations of those elements and compounds which trees utilize in their metabolism or which are toxic to trees. These environmental factors have to be described by a vector consisting of several components. For example, the number of macronutrients is nearly ten and also the number of

potentially toxic compounds is numerous.

Environmental factors vary within both space and time. While the spatial properties of the light climate (e.g., Ross 1981, Oker-Blom 1986) and the seasonal and diurnal changes in temperature are well known, the ecological implications of these variations are problematic. Concentrations of nutrients and toxic substances vary strongly with space and time, introducing large variation. Thus the environment u should ideally be determined at each point in space x and time t. For practical measurements the environment is treated in a small spatial and temporal volume element.

Matter is transferred among the following components of the ecosystem: atmosphere, vegetation, soil, groundwater, and surface waters (Figure 1). The system includes sources and sinks. Matter is introduced into circulation by, e.g., weathering processes and leaves the cycle by leaching and sedimentation. Sedimentation occurs to subsoil and to the bottom of surface waters. Weathering of minerals and volcanic activity constitute the most important sources of matter. It is important to note that the concentrations of the circulating species are determined by the flow rates of the dispersion media, by the rates of weathering and sedimentation, and by the rates of internal biogeochemical transformation processes.
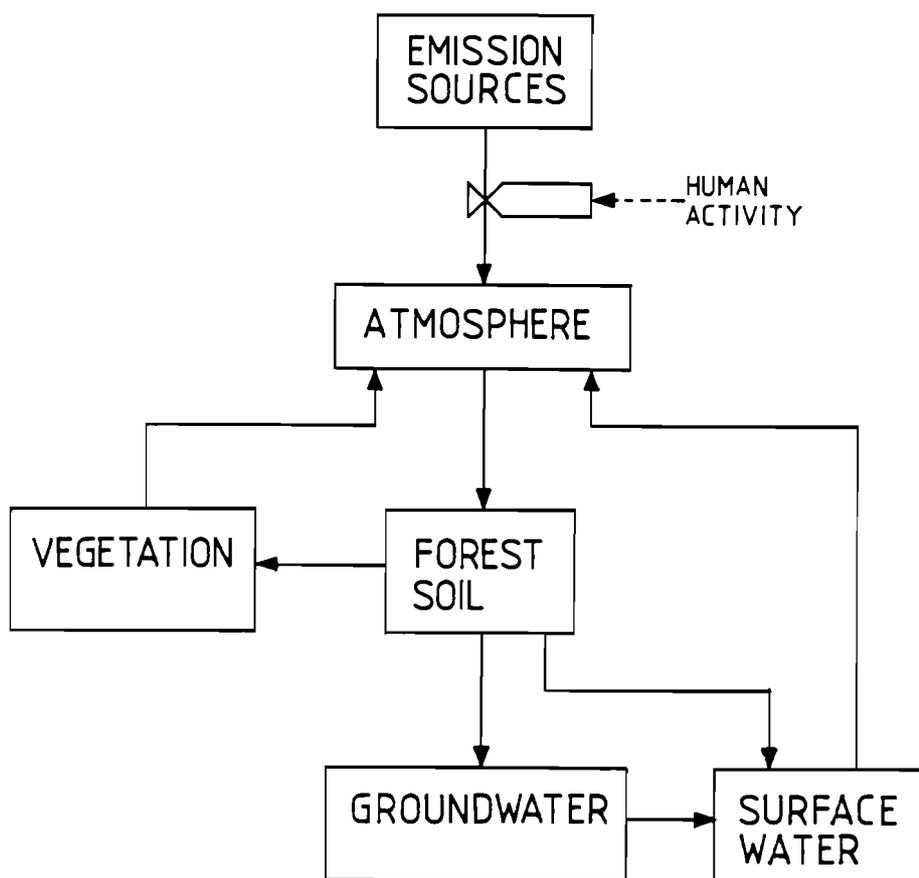

Figure 1. Mass fluxes in the ecosystem. Chemical compounds (CO_2, SO_2, NO_x, O_3, H^+, Ca^{++}, Mg^{++}, K^+) are transported with air and water and participate in biogeochemical processes within the ecosystem. The arrows represent mass fluxes of air, water and chemical species. The direction of the arrows represents the predominant direction of water flow.

In the following, a method for quantitative description of the dynamics of the plants' microenvironment is outlined. Space and time are subdivided into volumes and intervals so small that each subvolume during each time interval can be considered homogeneous with respect to the compound of interest. The amount of the compound in the subvolume can change due to in- and outflow and by internal processes that produce or consume the compound.

Let $M_i(\Delta V, t)$ denote the amount of compound i in the subvolume ΔV at the moment t. Let $Q_i(V, t)$ denote the inflow of the compound i into the subvolume and $Q_i(V+\Delta V, t)$ denote the outflow of the same compound. Furthermore, let $R_i(\Delta V, \Delta t)$ denote the internal production and $S_i(\Delta V, \Delta t)$ the internal consumption of the compound i in the subvolume ΔV during the time interval Δt. The spatial coordinate is x and Δx is the increment in the direction of the predominant flow. The volume increment ΔV is chosen so that one of its sides is perpendicular to Δx. The law of mass conservation applies to all environmental factors except irradiance and temperature. Thus, the change in amount of some compound in the subvolume ΔV during the time Δt equals inflow minus outflow plus internal production minus internal consumption.

$$M_i(\Delta V, t+\Delta t) - M_i(\Delta V, t) = Q_i(x,t) - Q_i(x+\Delta x,t) + R_i(\Delta V, \Delta t) - S_i(\Delta V, \Delta t) \quad (1)$$

If the transport processes in the air or water are modeled in addition, then the amounts in each subvolume and at each moment can be determined using Eq. (1). The spatial and temporal behavior can be calculated by, for example, numerical approximation. If the transport system is well known, Eq. (1) takes the form of a partial differential equation. When the transport medium can be assumed homogeneous, the parameters of this partial differential equation can be lumped, resulting in an ordinary differential equation.

As far as is known from historical data, climate and matter fluxes have been changing at least within the time span of a few thousand years. In shorter intervals there are random fluctuations around a constant mean value. The atmospheric CO_2 concentration has been rather stable after the Ice Age until the last century. The concentrations of macronutrients, e.g., potassium and calcium, have also been rather constant in nordic podzolic soils during the same period. It can be estimated that during this stable period the vegetation has adapted to the prevailing environmental conditions.

The system is not, however, stable any more since the flow of several compounds from the surface of the earth into the atmosphere has been increasing during the last century with the use of fossil fuels (Figure 2). The chemical and physical properties of the atmosphere have been changing because the composition of the atmosphere has changed due to increased inputs and these changes have generated changes in the flow from the atmosphere to forests and forest soils. Thus, the environmental factors are changing.

2.2. Atmospheric Environment

Plants assimilate carbon dioxide from the atmosphere in the process of photosynthesis. At prevailing ambient concentrations, 350 ppm (430 mg m^{-3}), the CO_2 concentration strongly limits photosynthesis, especially at high irradiance. Thus any increase in the availability of CO_2 will have a considerable effect on plant production. Among the anthropogenic emissions to the atmosphere, CO_2 is dominating. CO_2 is very inert and reacts only with few substances in the atmosphere. Spatial variations in CO_2 concentrations are small and thus their time development can be studied on a global scale.

Sulphur dioxide is one of the most abundant toxic compounds in anthropogenic emissions. It is reactive in the atmosphere, transforming readily to particle compounds, especially with water vapor. Its transformation time in the atmosphere is in the order of days. Due to its reactivity sulphur is removed from the atmosphere differently than CO_2. The main mechanisms are wet and dry deposition.
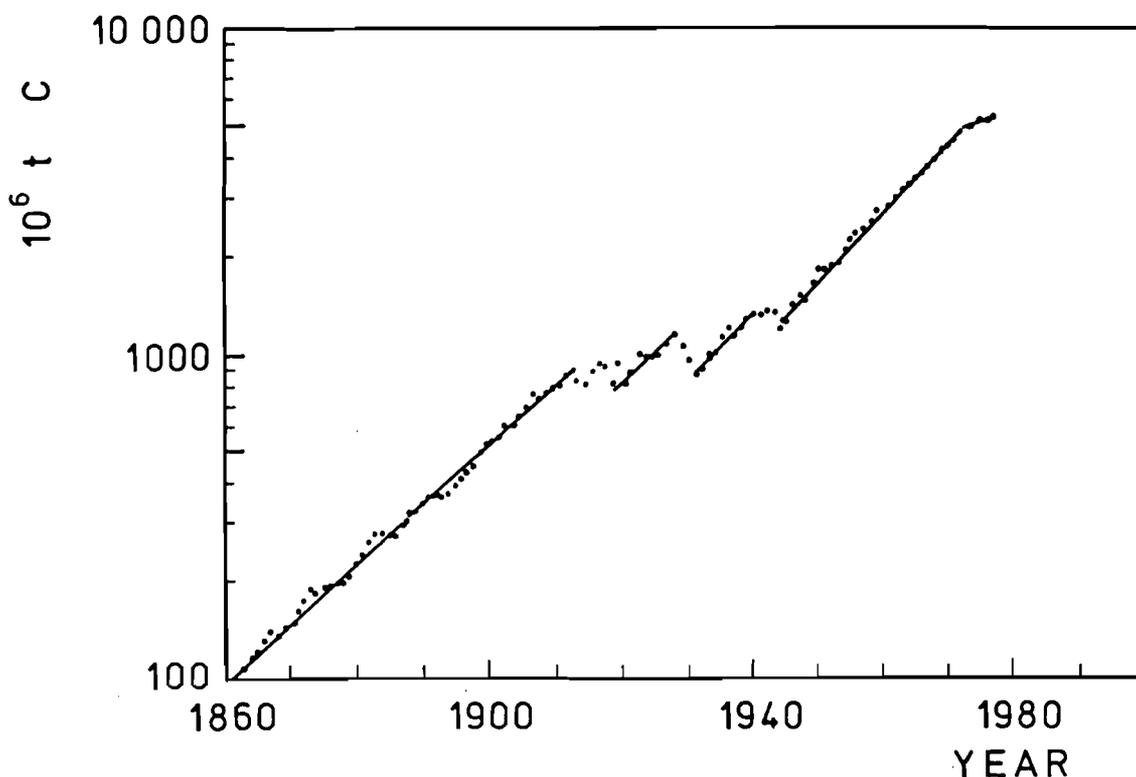
Figure 2. Temporal development of worldwide use of fossil fuels. CO_2 from fossil fuels according to Keeling (1973).

The spatial variation of SO_2 emissions and partly also sulphur deposition is pronounced, especially at the regional scale. Thus a rather small volume element is needed in the analysis. It is possible to model the time development and spatial variation of SO_2 using the volume-element approach. The result, however, covers generally only an episode and a restricted area. High concentrations of SO_2 are found only close to the major emission sources, for instance, in central Europe. The levels of SO_2 in remote areas such as northern Scandinavia are low, although increasing. Concentrations of sulphate and nitrate in Greenland ice-cores have been shown to have doubled from 1895 to 1978 (Neftel et al. 1985).

Nitrogen oxides are emitted in combustion of fossil fuels in energy production and traffic, and ammonium is produced in large amounts in agriculture and in natural bacterial action. NO_x is transformed to nitric acid in the atmosphere, thus contributing to the acidity of rain. NO_x are also precursors of ozone. The chemistry of NO_x in the atmosphere is complicated as a large number of formation and decomposition reactions are involved. The residence time of NO_x is short. The atmospheric distribution of NO_x is nonuniform. Calculations of spatial and temporal variations in ambient NO_x concentrations are therefore cumbersome and prediction of long-range transport of nitrogen is still a subject for discussion (Grennfelt et al. 1987). The behavior of NO_x and SO_2 is summarized in Table 1.

Table 1. Dispersion and transformation of chemical species in terms of spatial and temporal scales. Adapted from Grennfelt et al. (1987) and Seinfeldt (1986).

Species	Space (Grennfelt)	Time (Grennfelt)	Residence Time (Seinfeldt)
NO	1 km	< 1 h	
NO_2	some 100 km	2 d	
$NO + NO_2$			1 d
HNO_3			1 d
SO_2	some 100 km	2 d	40 d
SO_4^{2-}	1000 km	5d	

Ozone is formed in the atmosphere in reactions of nitrogen oxides and carbon species, especially hydrocarbons, carbon monoxide and aldehydes under the effect of solar energy. The key role is played by the hydroxyl radical. Ozone is very active and consequently its concentration varies considerably. The volume element must be chosen so that no considerable variation of hydrocarbons, nitrogen oxides or O_3 appears. The spatial requirement now becomes very strict because of the high variability of the hydrocarbon substances. Because vegetation emits hydrocarbons, greater amounts of ozone than expected may be formed (Atkinson et al. 1984) and cycled very close to the leaf surface. Ozone is toxic to plants. Because of complex ozone chemistry in the air, the effects of ozone on trees are difficult to quantify at the moment.

2.3. Soil Environment

A forest soil develops through processes of chemical, physical and biological weathering of the parent material, dissolution and precipitation of minerals, and formation of organic complexes. The rate of soil formation and the characteristics of the end product depend on the geochemical properties of the parent material, the climatic conditions, the vegetation, and the topography of the site.

Soil is a multiphase system consisting of a solid (ca. 50% by volume), a gaseous (10–40% by volume) and an aqueous phase. The solid phase consists of colloids and larger particles of minerals and dead organic material. The reactive surface of the solid phase is very large, ranging from a few square meters to some 500 m^2 g^{-1} (Scheffer et al. 1982). The higher the clay and organic matter content, the larger is the specific surface of the soil. The gaseous phase consists of atmospheric constituents and volatile organic compounds. The main substance in the aqueous phase is water, with ionic species. The rate of cycling of elements in the different phases in the soil depends on the ionic concentrations of acids and bases in soil.

The method for describing the microenvironment of plants outlined in Chapter 2.1. was implemented for the soil environment. A dynamic model of transport and local processes in forest soil was developed in order to study the effect of ionic deposition and hydrology on the vertical distribution of ions in the soil profile (Holmberg et al. 1985b). The vertical transport of water in forest soil takes place through gravitational flow in micro- and macropores and capillary rise of water. Ions are transported vertically in soil by convective flow, i.e., mass flow with water, and by diffusive flow that arises from concentration

- 6 -

gradients in soil. Assuming a homogeneous soil, the diffusivity equation (e.g., Hillel 1971) can be used. It takes the form of partial differential equations (Appendix 1), which are solved numerically. This distributed model of the transport processes in soil may be simplified by lumping, or aggregating, the spatial characteristics.

The uptake of water by the roots is calculated from the evapotranspiration rate and the vertical distribution of roots. The weathering rate of minerals is assumed to increase with the distance from topsoil such that a total annual weathering of around 1 meq m^{-2} is obtained in the uppermost 0.5 m of mineral soil (Nilsson 1986).

The exchange of ions between soil solution and soil particles is a dynamic process, the rate of which was assumed to be determined by the equivalent concentrations of ions in solution and on soil particles. The rates of the exchange reactions are calculated from differential equations (Appendix 2). These equations are combined with the transport equations (Appendix 1) to give the vertical distributions of ions in soil.

The distributed model was used to study the impact of water uptake on the ionic concentrations in the profile. Drying out of topsoil as a consequence of water uptake by the roots with a mass peak at 0.05 m below the surface of the soil was simulated. Transpiration results in an increase in the ion concentrations in the soil solution and intensifies the ion exchange between soil solution and soil particles. Figures 3a and 3b show the vertical distributions of hydrogen ions and base cations after 100 h of drought. The initial distributions of ions were uniform.

3. EFFECT ON STAND DEVELOPMENT

3.1. Functional Basis of Stand Development

Plants extract material from the environment and process it through metabolic processes. Carbon dioxide, water and nutrients (e.g., N, K, Mg, Ca, P) are the most important compounds in the flows to the plants. In addition plants transpire large amounts of water. For each main metabolic process there exists a specialized tissue; leaves account for photosynthesis, fine roots for uptake of water and nutrients, and coarse roots, stem and branches for water transport. The flows within a plant are thus diverse.

All functioning requires energy. The energy for metabolism is converted to usable form in photosynthesis when carbohydrates are formed from carbon dioxide and water using light as the primary source of energy. The energy from solar radiation, more specifically irradiance, is the dominant environmental factor affecting photosynthesis in field conditions (Hari et al. 1981). The low level of CO_2 available in the atmosphere limits photosynthesis, especially at high irradiance. The structure of leaves is such that the intake of CO_2 is associated with the transpiration of water. The amount of transpired water is usually about a hundredfold greater than the amount of photosynthetic products.

Large amounts of water, taken up by fine roots during transpiration, transports dissolved nutrients from the soil to the trees. This source is not sufficient, however, and nutrients are actively extracted from the surface of soil particles. Carbohydrates are used for root growth and for the functioning of ion pumps.

Growth models are very sensitive to the allocation of carbohydrates to leaves, fine roots and the transport system. In an optimal functional structure the capacity of roots to supply water and nutrients is balanced with the need of other organelles, and parts of the water transport system are balanced with each other and with the need of the leaves. It is evident that evolutionary pressure has been strong to develop effective allocation in trees.
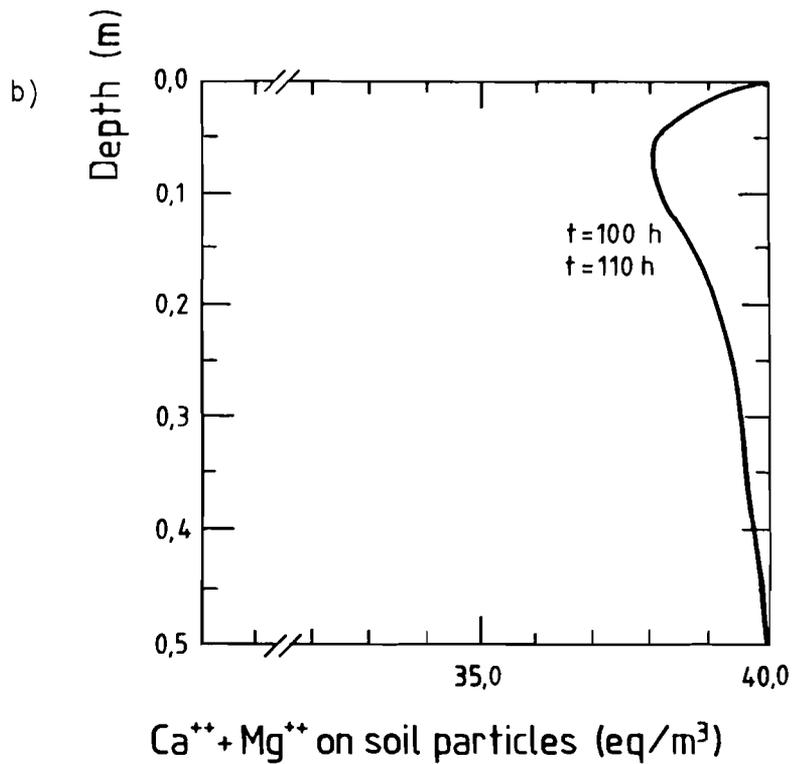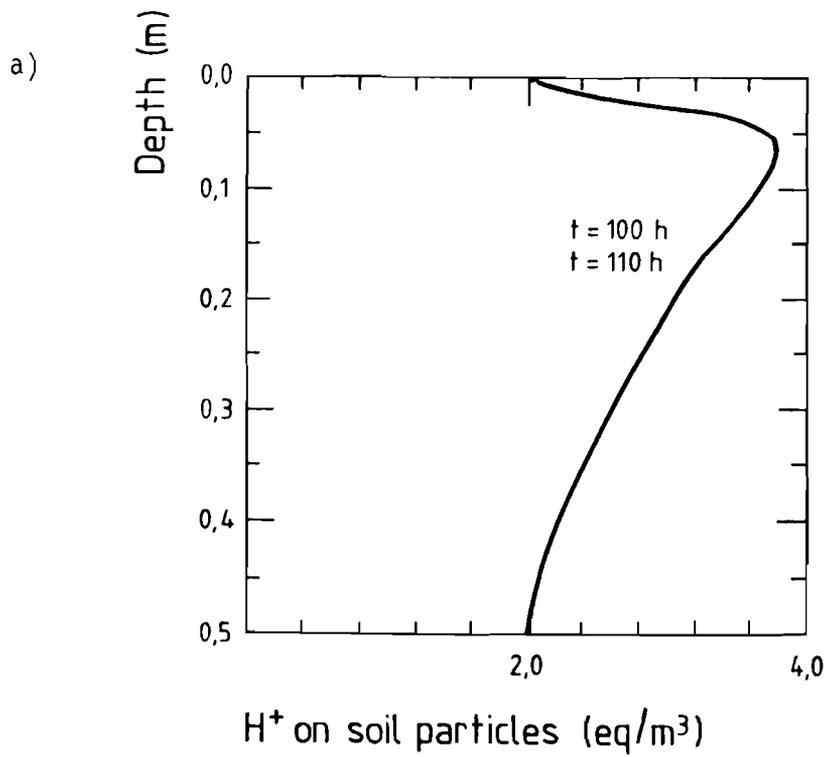
Figure 3. Simulated vertical profiles of hydrogen ions (a) and base cations (b) adsorbed to soil particles following a period of 100 h of high transpiration (1.5 mm h^{-1}) (Holmberg et al. 1985b).

3.2. Aggregation

Field measurements have shown that the dependence of photosynthetic rate on environmental factors is simple and strong (Hari et al. 1981). Let p denote photosynthetic rate $(g\ g(needle)^{-1}\ s^{-1})$ and ρ_n leaf mass distribution $(g(needle)\ m^{-3})$. The annual amount of photosynthetic production $P(t_k)$ during the kth year is obtained by integration as follows:

$$P(t_k) = \int_V \int_{t_k}^{t_{k+1}} \rho_n(x)\ p(x,t)\ dtdV \qquad (2)$$

where V is the volume of the tree under consideration. A multiplicative model has proved applicable in the analysis of photosynthetic rate, i.e.,

$$p(x,t) = p_0 f_1(u_1(x,t))\ f_2(u_2(x,t)) \qquad f_n(u_n(x,t)) \qquad (3)$$

where the function f_i, $i = 1,2,...,9$, is the impact of the environmental factor i on photosynthetic rate. This function can be quantified with measurements of photosynthesis and environmental factors. The parameter p_0 describes the value of maximal photosynthetic rate $(p_0 = 6$ g dry matter $(g\ needles\ *\ h)^{-1})$. The function f_i, $i = 3,...,9$, is normalized in such a way that it equals unity in the conditions before apparent anthropogenic influence on the environment.

We define the relative annual effect of environmental factors on photosynthesis during the kth year $U^P(t_k)$ as the ratio of the amount of photosynthesis during the year k to that amount the same needle system would have been able to form in conditions before anthropogenic influence on environmental factors.

The relative annual effect of the environment on the photosynthesis $U^P(t_k)$ can now be determined using Eqs. (2) and (3).

$$U^P(t_k) = \frac{\int_V \int_{t_k}^{t_{k+1}} \rho_n(x)\ f_1(u_1(x,t)) \cdots f_n(u_n(x,t))\ dtdV}{\int_V \int_{t_0}^{t_1} \rho_n(x)\ f_1(u_1(x,t)) \cdots f_n(u_n(x,t))\ dtdV} \qquad (4)$$

Although the above equation is operational in principle, it is rather complicated to use in practice. The following approximation is, however, sufficiently accurate. We define the annual impact $U_i^P(t_k)$ of the ith environmental factor on the photosynthetic rate as follows:

$$U_i^P(t_k) = \frac{\int_V \int_{t_k}^{t_{k+1}} \rho_n(x)\ f_i(u_i(x,t))\ dtdV}{\int_V \rho_n(x)\ dV} \qquad (5)$$

Multiplication of the effects of each component of the environmental vector gives a sufficient estimate of the relative annual impact of the environment on the photosynthetic rate

$$U^P(t_k) = \Pi\ U_i^P(t_k) \qquad (6)$$

We can now consider the different factors in some detail. The increase in atmospheric CO_2 concentrations is the most important change in environmental factors on a global scale. We denote the atmospheric concentration of CO_2 by u_3. The dependence of the photosynthetic rate on the CO_2 concentration is linear at concentrations below 400 ppm. The response saturates at high CO_2 concentrations. When the dependence of photosynthetic rate on u_3 depicted in Figure 4 is applied in determining U_3^P, the time development of Figure 5 is obtained. Consequently, increasing the concentration of CO_2 causes a major change in the global photosynthetic production.
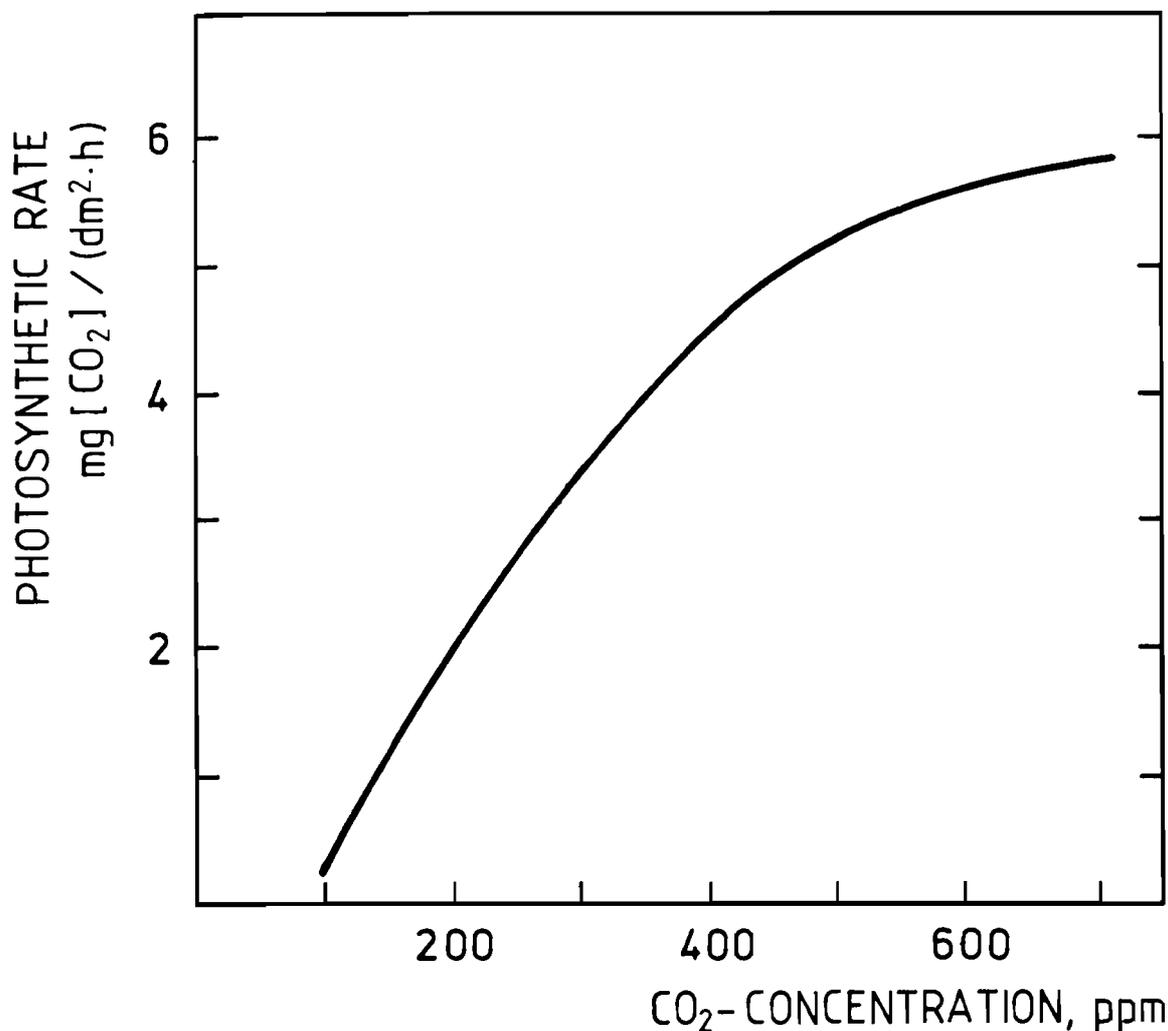
Figure 4. Dependence of photosynthetic rate on atmospheric CO_2 concentration. Measured in Hyytiälä, central Finland, 1982. Light intensity 630 $\mu E\ m^{-2}\ s^{-1}$, temperature 17.5° C.

The other atmospheric compounds cause principally only local effects on photosynthetic production, since these compounds are chemically very reactive. Ozone may be produced in toxic amounts near some leaves when the ratio of concentrations of nitrogen oxides to hydrocarbons is at the right level. This happens mainly in the vicinity of emission sources.

The relative annual effect of environmental factors on nutrient uptake in the kth year $U^N(t_k)$ is defined as the ratio of the amount of nutrient uptake during that year to the amount that could have been taken up by the same root system under conditions of no anthropogenic emissions. The process of nutrient uptake is less well understood in quantitative terms than photosynthesis. However, the same approach in quantifying U^N can be applied but the results are more uncertain.
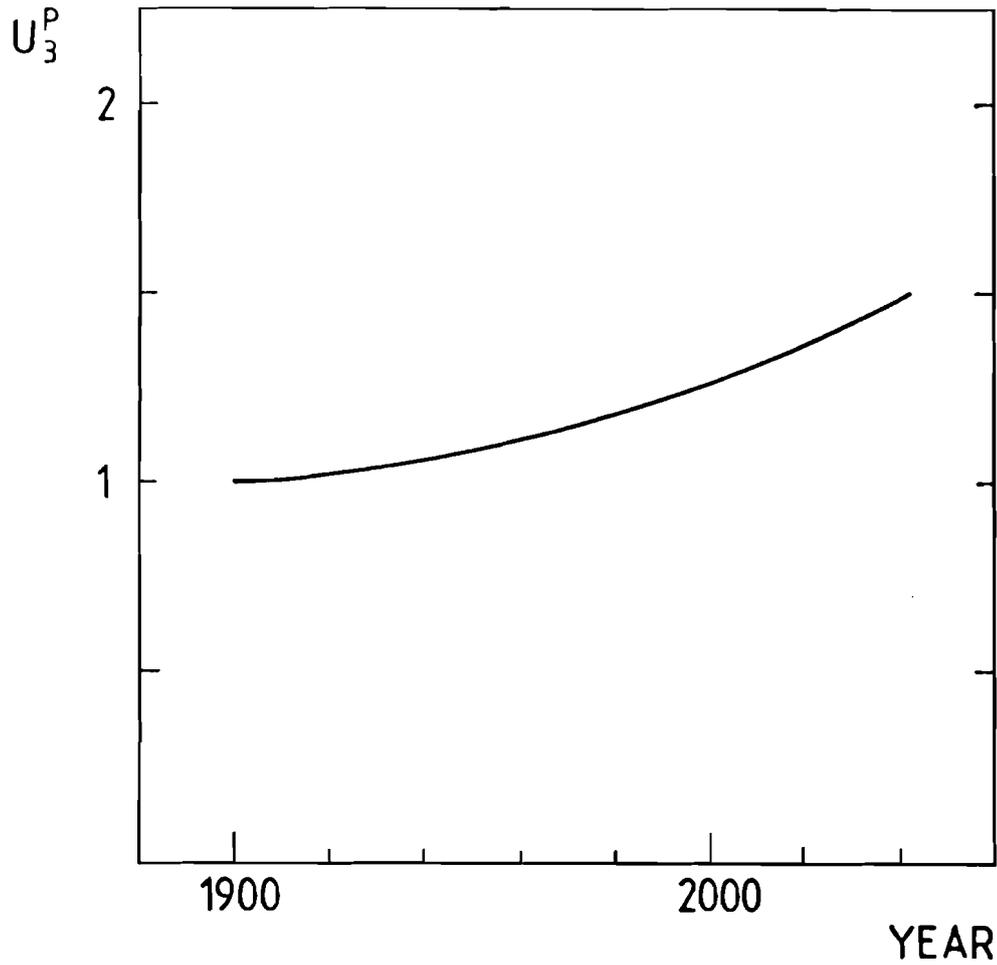
Figure 5. Annual impact of CO_2 on photosynthetic rate, assuming a conservative prediction of a linear increase in atmospheric CO_2 concentrations.

Let r denote nutrient uptake rate and ρ_r the root density in the soil. The relative annual effect on nutrient uptake can be quantified as follows:

$$U^N(t_k) = \frac{\int_V \int_{t_k}^{t_{k+1}} \rho_r(x)\, r(u(x,t))\, dt dV}{\int_V \int_{t_0}^{t_1} \rho_r(x)\, r(u(x,t))\, dt dV} \tag{7}$$

The nutrients can be either in the soil solution or on soil particles. Assume that the nutrient uptake rate is a saturating function of concentrations in the soil solution and on soil particles:

$$r(u_8(x,t),\, u_9(x,t)) = \frac{r_{max}\,(au_8 + bu_9)}{(au_8 + bu_9 + c)} \tag{8}$$

- 11 -

The weights a and b are determined in such way that trees utilize the nutrients carried by the flow of water from the soil to the roots and then satisfy their remaining need of nutrients by uptake from the surfaces of soil particles.

The analysis of nutrient concentrations as functions of space is too detailed for this purpose. The soil model in Chapter 2.3. can be simplified by aggregating with respect to the spatial variability. The resulting lumped model is delineated in the following. Denote the hydrogen ions and base cations in the soil solution as $u_6(t)$ and $u_8(t)$, and hydrogen and base cations adsorbed on soil particles as $u_7(t)$ and $u_9(t)$. Since spatial variability is not considered, the concentrations are only functions of time ($u_6(x,t) = u_6(t)$, etc.). The fluxes $q_6(t) = q_6(0,t)$ and $q_8(t) = q_8(0,t)$ represent the total external input by dry and wet deposition of hydrogen ions and base cations K, Mg and Ca.

The water fluxes in the soil are denoted by q_{10}. Here $q_{10}(0,t)$ is the rate of rainfall, or the flow of water to the surface of the soil, and $q_{10}(L,t)$ is the rate of leaching to groundwater, or the flow of water at depth L. Assuming no surface runoff, the change in water content $u_{10}(t)$ in the profile can be expressed by the equation

$$\frac{du_{10}(t)}{dt} = q_{10}(0,t) - q_{10}(L,t) - s_{10} \tag{9}$$

where s_{10} represents the rate of evapotranspiration. We make the simplifying assumption that the water content does not change, i.e.,

$$\frac{du_{10}(t)}{dt} = 0 \tag{10}$$

This gives an approximation for the rate of leaching

$$q_{10}(L,t) = q_{10}(0,t) - s_{10} \tag{11}$$

i.e., the rate of leaching equals precipitation minus evapotranspiration.

The changes in the amount of hydrogen ions and base cations in the uppermost mineral soil layer of thickness L can be formulated using expressions for the transport and the exchange reactions and weathering.

$$\frac{du_6(t)}{dt} = q_6(t) - \frac{q_{10}(L,t)\, u_6(t)}{u_{10}(t)\, L} + s_6 \tag{12}$$

$$\frac{du_7(t)}{dt} = s_7 \tag{13}$$

$$\frac{du_8(t)}{dt} = q_8(t) - \frac{q_{10}(L,t)\, u_8(t)}{u_{10}(t)\, L} + s_8 \tag{14}$$

$$\frac{du_9(t)}{dt} = s_9 \tag{15}$$

where the rates of ion exchange s_6, s_7, s_8, and s_9 are calculated as in Appendix 2.

In the soil model it is assumed that the rate of cation exchange depends on the equivalent concentrations of ions in soil solution and on the exchange sites, and that the rate of weathering is independent of these concentrations. Furthermore, surface runoff is assumed not to take place, i.e., the rate of water percolating through soil equals precipitation minus evapotranspiration.

The lumped soil model was used to simulate the impact of changing atmospheric deposition of hydrogen ions. Starting from the year 1900 with a deposition of hydrogen ions and base cations below 5 meq m^{-2}, the deposition was assumed to peak in 1970 (25 meq m^{-2} H$^+$ and 5 meq m^{-2} Ca^{++} + Mg^{++} + K$^+$) and thereafter decrease by 30% by the

year 1995. The deposition peak in 1970 is reflected in the concentrations of hydrogen ions and base cations in soil solution (Figure 6a). This input of H^+ results in a depletion of base cations from the exchange sites on the surface of the soil particles (Figure 6b).

Toxic compounds may also cause direct damage to leaves and roots. Let $U_n^D(t_k)$ denote the degree of damage of the leaves and $U_r^D(t_k)$ that of the roots in the kth year. Let h denote the rate of damage. The degree of damage is obtained analogously to $U^P(t_k)$ and $U^N(t_k)$ by integration

$$U_n^D(t_k) = \int_V \int_{t_k}^{t_{k+1}} \rho_n(x) \, h_n(u(x,t)) \, dtdV \qquad (16)$$

$$U_r^D(t_k) = \int_V \int_{t_k}^{t_{k+1}} \rho_r(x) \, h_r(u(x,t)) \, dtdV \qquad (17)$$

The rates of damage h_n and h_r and their dependence on environmental factors are not well known.

3.3. Stand Development

Process-based, causal stand growth models constitute an operational framework for assessing the effects of changing environmental factors on forest growth. This type of modeling is gaining increasing attention (c.f. McMutrie and Wolf 1983, Mäkelä and Hari 1986, and Mohren 1987). Our stand model (Mäkelä and Hari 1986) considers several size classes in the stand. The size classes interact with each other through shading, which reduces photosynthetic production. Annual amounts of photosynthetic production are allocated to needles, branches, stem, and roots. In the latest version of the stand model (Hari et al. 1985, Mäkelä 1986), the dynamics of carbohydrate allocation are formulated on the basis of regularities in the structure of a tree.

Let $M_n(t_k)$ denote the needle mass in a tree during the kth year, $P(t_k)$ the amount of photosynthesis and A_n the coefficient of allocation of photosynthesis to needles. Let $M_r(t_k)$ denote the root biomass and A_r the allocation of photosynthates to roots. It is noted that the amount of nutrients supplied by roots should fulfill the foliage's need of nutrients. The stand model links consequent years as follows:

$$M_n(t_k) = F(P(t_k-1), M_n(t_k-1), A_n(t_k-1)) \qquad (18)$$

$$M_r(t_k) = G(P(t_k-1), M_r(t_k-1), A_r(t_k-1)) \qquad (19)$$

$$M_r(t_k) = \gamma \, M_n(t_k) \qquad (20)$$

The effect of environmental factors, such as CO_2 and soil fertility, are not treated in the above stand model; it is implicitly assumed that they do not change with time. This implicit assumption has no justification any more. The stand model should be developed, however, to include the effect of such changes.

Changes in the environmental factors generate changes in the metabolic rates and in the amounts of metabolites produced during a summer. The annual relative effect on photosynthesis $U^P(t_k)$, annual relative effect on nutrient uptake $U^N(t_k)$, degree of needle damage $U_n^D(t_k)$ and degree of root damage $U_r^D(t_k)$ are defined for use in the stand model. If we assume that the functioning principles of the stand do not change due to changes in environmental factors, but that metabolic rates do change, then the model structure remains the same. Consequently, the functions in Eqs. (18) and (19) do not change but the amounts of metabolites have to be replaced as follows:

$$M_n(t_k) = F(U^P(t_k-1) \, P(t_k-1), (1 - U_n^D(t_k-1)) \, M_n(t_k-1), A_n(t_k-1)) \qquad (21)$$

$$M_r(t_k) = G(U^P(t_k-1) \, P(t_k-1), (1 - U_r^D(t_k-1)) \, M_r(t_k-1), A_r(t_k-1)) \qquad (22)$$
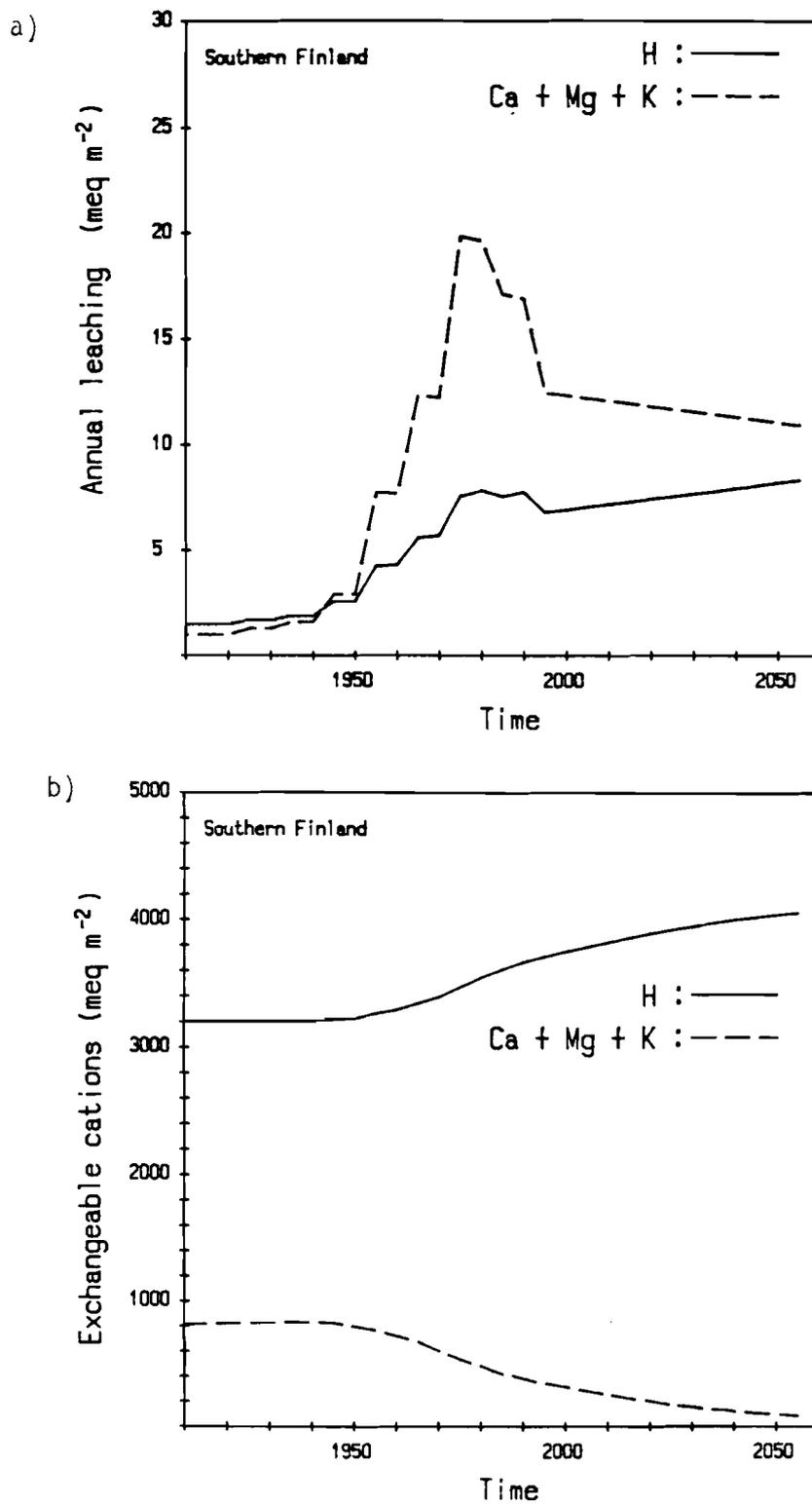
a)

b)

Figure 6. Simulation of the impact of acid deposition on forest soil. (a) Leaching of base cations to groundwater. (b) Depletion of base cations on exchange sites (Holmberg et al. 1985a).

$$M_r(t_k) = \gamma \, M_n(t_k)/U^N(t_k) \tag{23}$$

The model outlined above includes several details which are rather poorly known, and many parameter values used are inaccurate. The behavior of the stand model in its two forms has been demonstrated using the parameter values in the simulations corresponding to a moderately poor site in southern Finland (Figures 7 and 8).

The stand development in a static environment is characterized by a rapid increase in needle mass in early stand age. Later the needle mass begins to decline due to increasing allocation to the water transport system and respirational losses. The development of fine root mass follows the pattern of needle mass. On the other hand, in a dynamic environment the decreasing availability of cations causes an increasing allocation to the roots, which is reflected in a decrease of needle mass, stem volume and number of trees. The effect of CO_2 fertilization can be seen as a temporary increase in needle mass and stem volume in the early phase of stand development. The changes in the soil seem to be dominating in the present simulation example (Figures 7 and 8).

4. REGIONAL FOREST GROWTH

Our knowledge of stand development is considerable but too detailed for strategic decision making. Analysis and scenarios of forest growth at a national scale are needed for emission control. One way to produce information at the national scale is to base it on simulations at the level of the stand. This would, however, take too long in the present situation in which decisions about the reduction of emissions are urgently needed.

The scaling-up from a forest stand to a regional or national scale of forest growth is a problem of aggregation. Description of the environment and structure of forests at a national level has to be done in less detailed terms in order to facilitate the analysis. The spatial aggregation of environmental factors can either be done by using spatial mean values of environmental factors or by using the distributions of environmental factors within the area. Forest production then is obtained by integration over the distribution. The use of spatial distributions evidently results in more reliable estimates than the use of mean values.

Aggregation of the structure of forests is possible if the age structure of the forests in a region does not change. This requirement is fulfilled in forests that are treated on the basis of sustained yield or if they are completely natural, i.e., climax communities. The principle of sustained yield is largely accepted as the basis of forestry in industrialized countries. Assuming that the age structure of forests does not change on a regional or national scale, the relative analysis of the changes of forest growth per unit area is sufficient.

Let Y denote the time development of forest growth in the region under consideration. Divide the area into N classes according to the environmental factors. Let $g_j(u(t))$ denote the time development of relative forest growth in the jth subarea, A_j the area, V_j mean volume growth, and u^j the state of the environment in the jth subarea.

$$Y = \Sigma \, A_j V_j g_j(u^j(t)) \tag{24}$$

Forest growth in the subareas differs since the time development of the environmental factors differ. Analysis of the changes in the flows of compounds in the system formed by the atmosphere, forest soil, trees, and groundwater, gives the time development of the environmental factors for each subarea.

The determination of the growth g_j is problematic. In the long run it can be based on the behavior of the stand models. Rather rough estimates have to be applied at the present level of understanding of the dynamics of the change in environmental factors and its consequences for forest growth. A multiplicative model for linking the different components of the environment seems justified.
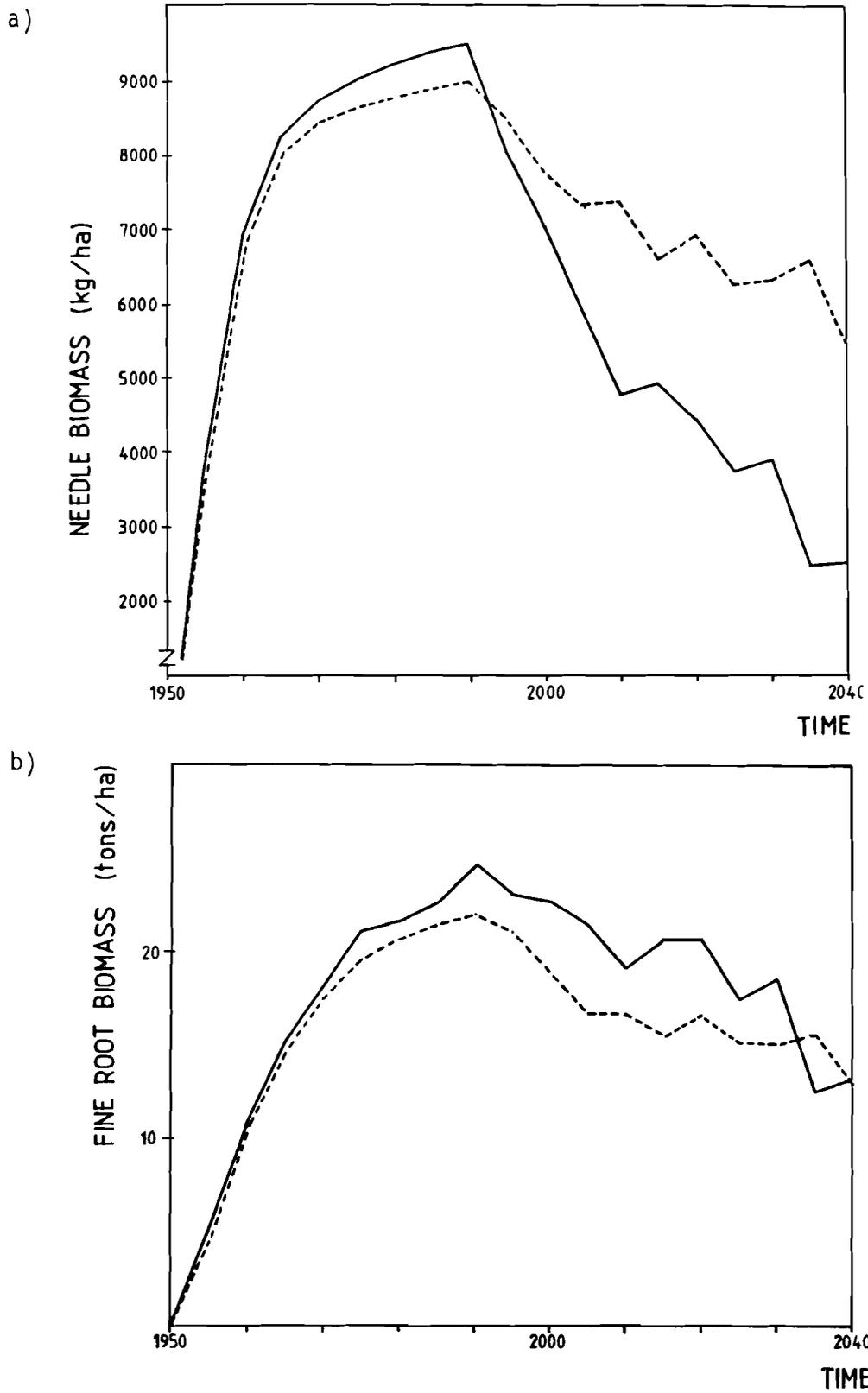
a)

b)

Figure 7. Simulated stand-level development of needle biomass (a) and root biomass (b) assuming a static (broken line) and a dynamic (thick line) environment.
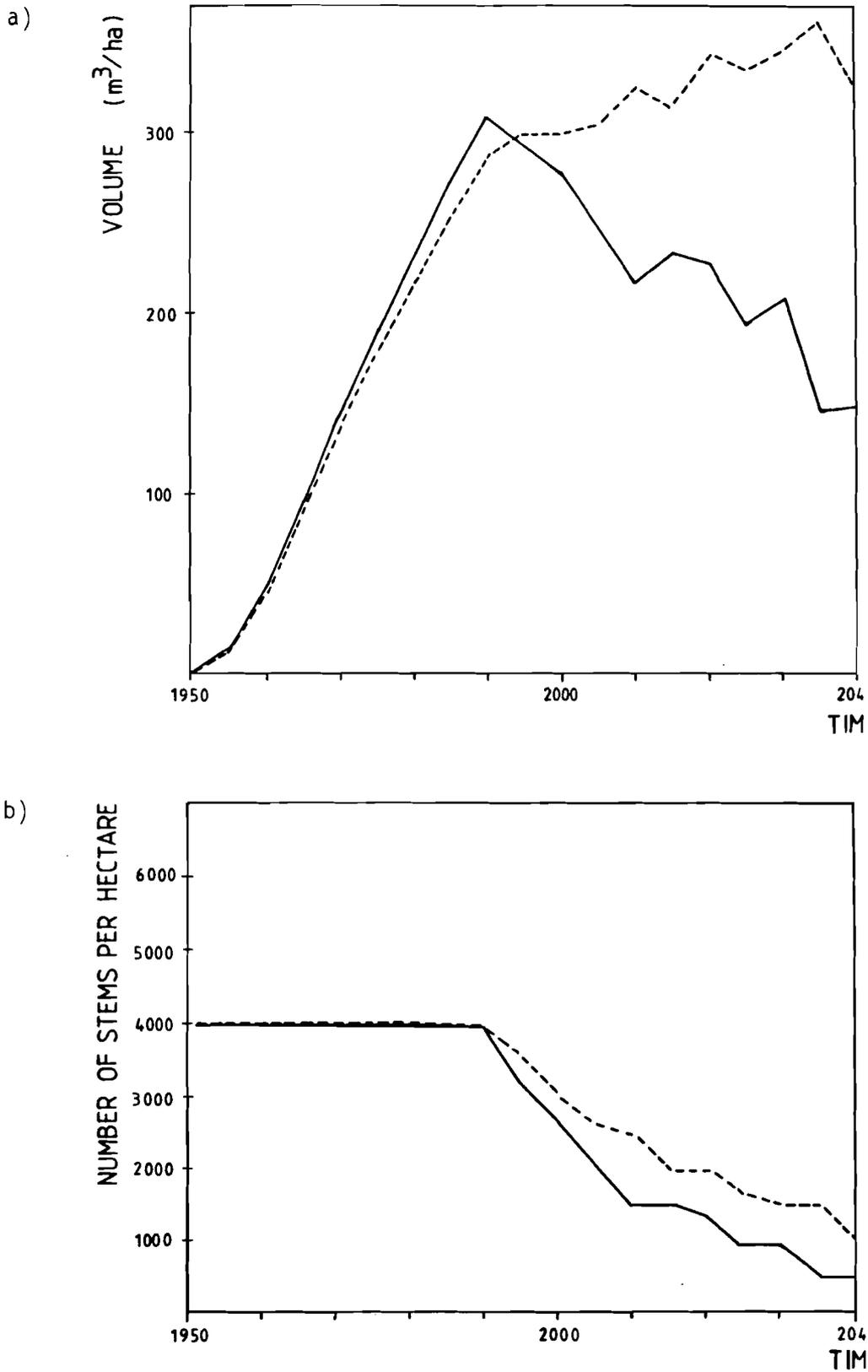
a)

b)

Figure 8. Simulated stand-level development of total stem volume (a) and number of trees (b) assuming a static (broken line) and a dynamic (thick line) environment.

The nutrient concentrations on soil particles and in the soil solution can be treated together since from these two sources nutrients are supplied to trees. Let u_8 denote the base cation concentration of the soil solution and u_9 that on soil particles. The trees transpire water around 100–1000 times their annual production of dry matter. This large amount of water carries nutrients, such as potassium, into roots. This amount of nutrients is not sufficient for trees growing on poor podzolic soil. Trees take nutrients from the surface of soil particles. We assume that these two sources of nutrients are equally important for the forest in the pre-industrialized situation. Let v denote the availability of base cations for trees. Assume that v can be obtained as a weighted mean of the concentrations in soil solution and on soil particles, i.e.,

$$v = \alpha \, u_8 + \beta \, u_9 \tag{25}$$

The weights α and β are determined in such a way that trees utilize the nutrients carried by the flow of water from the soil to the roots and then satisfy their remaining need of nutrients by uptake from the surface of soil particles.

Let u_3, u_4 and u_5 represent the atmospheric concentrations of CO_2, SO_2 and O_3, u_6 and u_7 the concentration of hydrogen ions in soil solution and on soil particles, and u_8 and u_9 the concentrations of base cations in soil solution and on soil particles.

The multiplicative approximation leads to the following model

$$g_j(t) = \Pi \, g^i(u_i^j(x,t)) \tag{26}$$

where g^i is the effect of the ith environmental factor on the growth. The determination of the functions has to be done with rather limited information, and only rough estimates can be obtained. A natural way is to estimate the effect of a change in a component of the environment on the metabolism of trees and then convert this change to growth. The metabolic processes considered are photosynthesis, nutrient uptake and allocation of carbohydrates.

The concentration of carbon dioxide affects photosynthesis, since CO_2 is the source of carbon for carbohydrates. The present low level strongly limits photosynthetic production. The dependence of photosynthetic rate on CO_2 concentration is easy to measure in the laboratory. We assume that the dependence of growth g_3 on carbon dioxide concentration is the same as that of the photosynthetic rate.

The effects of SO_2 and O_3 on growth are so weakly known at present that it is impossible to estimate the functions g_4 and g_5. Until more information is available, we assume that they equal one.

The amount of potassium in soil solution and on soil particles combines to describe availability v. In fertilization experiments in the 1960's it was observed that cation fertilization does not affect growth (e.g., Kukkola and Saramäki 1983). On the other hand, a severe potassium deficit is lethal for trees. We assume that a saturation function of the Michaelis–Menten type is a good approximation for the growth response to variable potassium availability.

$$g_8(t_k) = \frac{v(t_k)}{v(t_k) + \gamma \, v(t_0)} \tag{27}$$

The parameter $v(t_0)$ is the availability of potassium without anthropogenic emissions and γ is a scaling parameter.

The time development of deposition can be constructed using statistical information and scenarios of energy use, and measurements of deposition (Figure 9). When deposition is input into the models, the development of the environmental factors is obtained in each subarea and the time development of environmental factors can be converted into forest growth (Figure 10). The estimates of regional forest growth are obtained using Eq. (22).
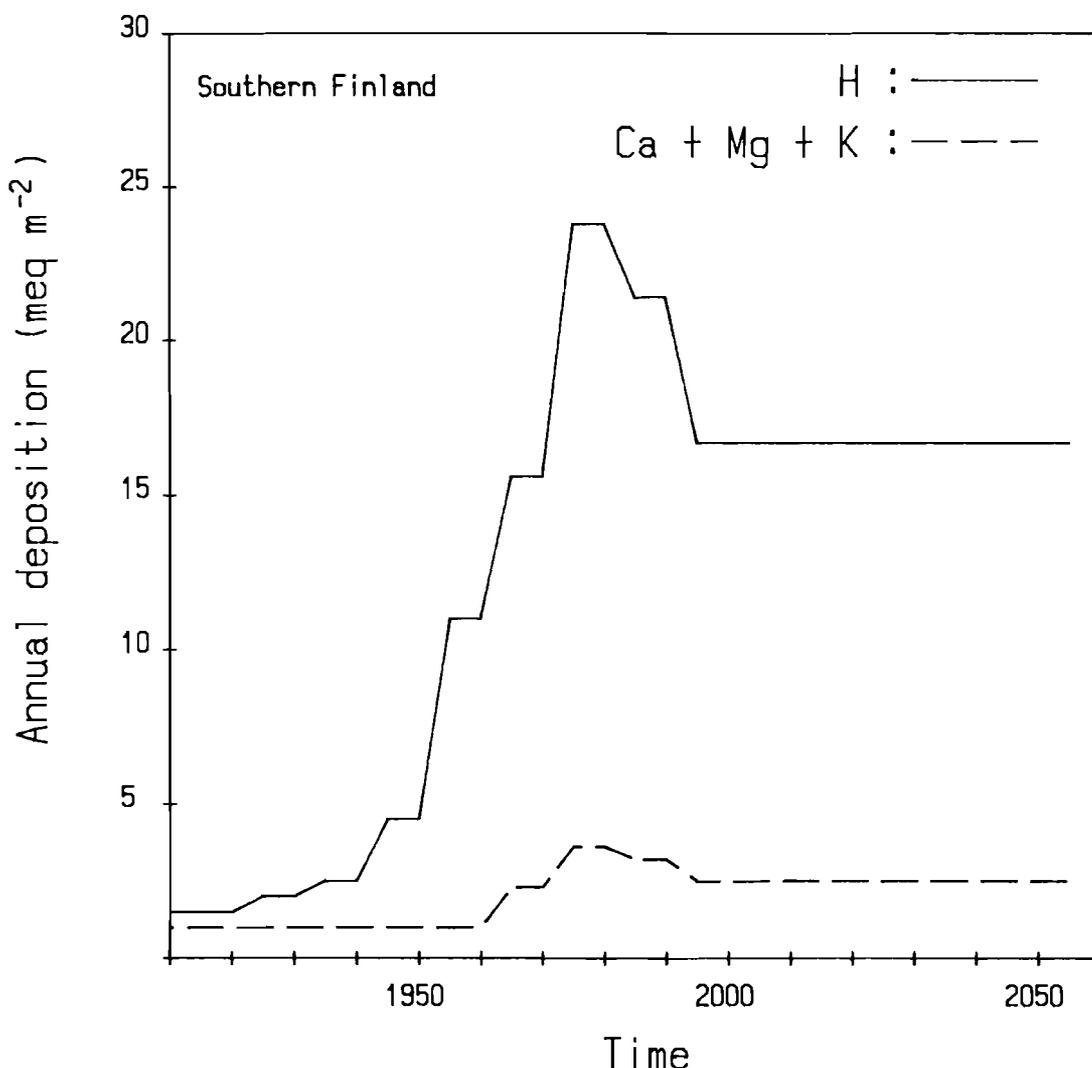
Figure 9. Temporal development of the deposition of hydrogen ions and base cations (Ca, Mg and K) in southern Finland. The peak of the 1970's is approximated from measurements by the Finnish Board of Waters (Järvinen and Haapala 1980). The deposition is assumed to follow the sulphur emissions in the period of 1900–1980. Furthermore, the present reductions of sulphur emissions are assumed to decrease the deposition by 30% of the 1980 value by the 1995.

5. CONCLUDING REMARKS

The analysis above is based on the flow of material in the system formed by the atmosphere, the forest soil, vegetation, groundwater, and surface waters. This starting point is very operational in the analysis, and a coherent set of models was constructed on the basis of the flows.

From an ecological point of view, the change in environmental factors is the most important result. The analysis shows that several concentrations of nutrients and toxic compounds are changing. Plants respond to this change of environmental factors. Forest growth is changing on a global scale. The assumption of an environment in a steady
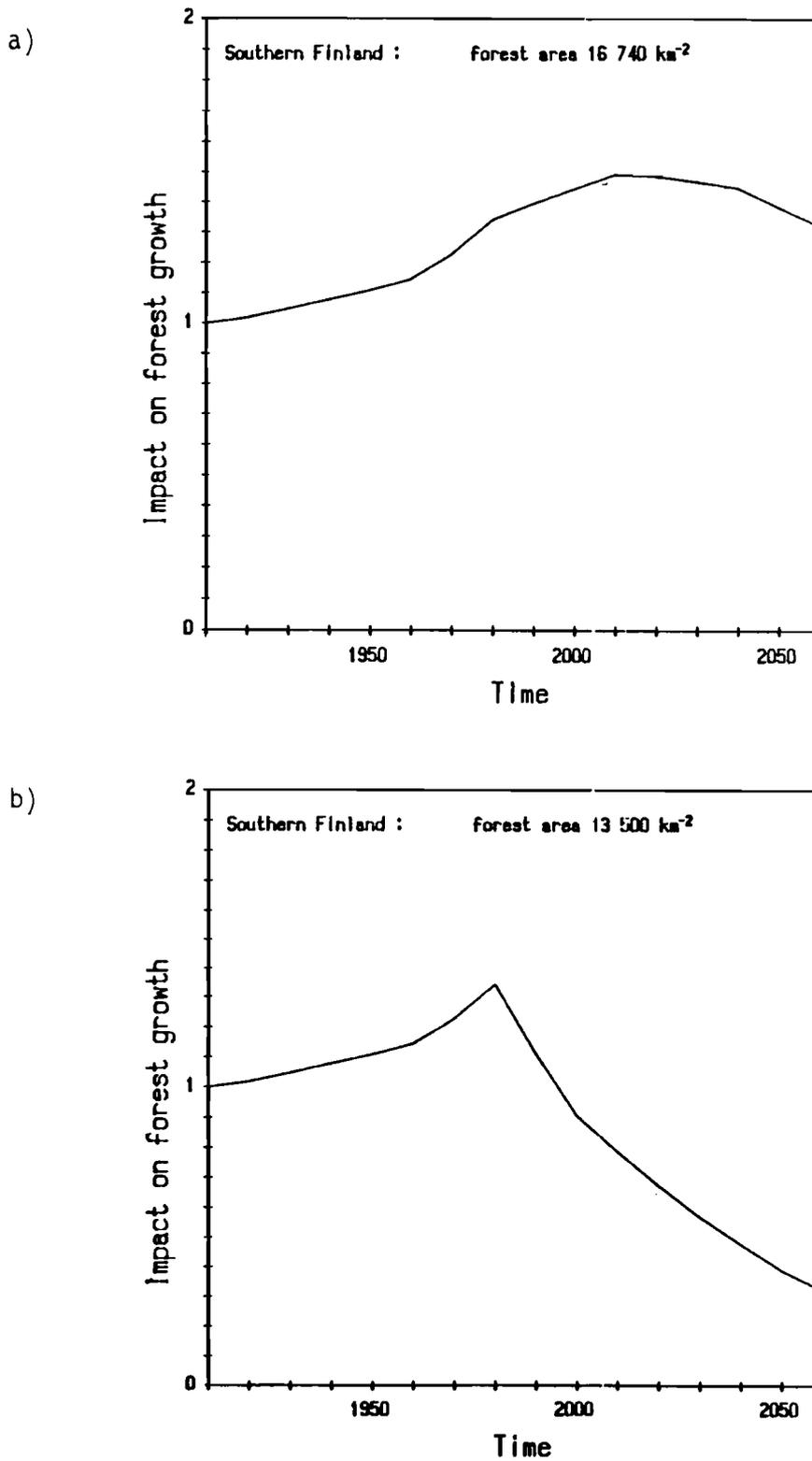
a)

b)

Figure 10. Temporal development of the impact on forest growth on two forest sites: (a) fertile soil with slow percolation; (b) poor soil with high percolation.

state, in which the environmental factors vary more or less randomly around a constant mean value, is implicit in many ecological studies. It appears to be no longer justified and calls for a revision of ecological research.

Aggregation or scaling-up is the most important methodological question in assessing the effects of changing environmental factors on the functioning of regional vegetation systems. It can be done either on a mathematical or on an ecological basis. When mathematical aggregation is applied, statistical mean values are usually used. This is the prevailing methodology used nowadays. Most measuring results are published only as mean values, monthly or daily. The plants do not, however, respond to mean values, but to the prevailing environment. The dependence of plant response to environmental factors is mostly nonlinear. The use of mean values leads to biased results if the response is nonlinear. This difficulty can be avoided if the aggregation is based on the analysis of the dependence of plant response as has been demonstrated in Eqs. (4)–(8) and (25)–(26).

There are several details in the analysis presented which are not sufficiently well known. Uncertainty about the deposition in forests, concerning especially base cations, the formation and levels of ozone near trees, the dependence of tree response on nutrient deficiency and toxic compounds in soils limit the analysis at present. The analysis can be applied as a tool to focus research on the relevant questions.

Forest decline is usually considered a phenomenom in heavily polluted areas in central Europe or in North America. However, we prefer to view forest decline as a symptom of a process in which the trees are responding to changes in their environment. It is remarkable that these changes and the consequent responses are no longer restricted to areas close to industrial activity. Such global and rapid environmental change as that which vegetation is presently experiencing has hardly ever occurred before.

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APPENDIX 1. Transport Processes in Soil. Flow Equations.

The processes of diffusive and convective flow of water and ions are formulated on the basis of the diffusivity equation (Hillel 1971). The parameters of the flow processes in soil are the hydraulic diffusivity $(D = 0.0012 \, \text{m}^2 \, \text{h}^{-1})$, the hydraulic conductivity $(K = 0.005 \, \text{m} \, \text{h}^{-1})$, the ion diffusivity $(C = 0.0012 \, \text{m}^2 \, \text{h}^{-1})$, and the porosity of the soil $(P = 0.6 \, \text{m}^3 \, \text{m}^{-3})$. Assuming a homogeneous soil, the Darcy flow equation can be used and the vertical distributions of the ionic concentrations can be calculated from the following partial differential equations, where $u_{10}(x,t)$ denotes water content of the soil, $u_6(x,t)$ and $u_8(x,t)$ denote the concentrations of hydrogen ions and base cations in soil solution, $u_7(x,t)$ and $u_9(x,t)$ are the concentrations of hydrogen and base cations absorbed to the exchanger. The mass fluxes are denoted by $q_{10}(x,t)$ for the flow of water, $q_6(x,t)$ and $q_8(x,t)$ for the flow of hydrogen ions and base cations in the liquid phase.

$$\frac{du_{10}(x,t)}{dt} = \frac{dq_{10}(x,t)}{dx} + s_{10} \tag{A1}$$

$$q_{10}(x,t) = -\frac{du_{10}(x,t)}{dx} + Ku_{10} \tag{A2}$$

$$\frac{du_6(x,t)}{dt} = -\frac{dq_6(x,t)}{dx} + s_6 \tag{A3}$$

$$q_6(x,t) = -\frac{Cdu_6(x,t)}{dx} + \frac{q_{10}(x,t) \, u_6(x,t)}{Pu_{10}(x,t)} \tag{A4}$$

$$\frac{du_8(x,t)}{dt} = -\frac{dq_8(x,t)}{dx} + s_8 \tag{A5}$$

$$q_8(x,t) = -\frac{Cdu_8(x,t)}{dx} + \frac{q_{10}(x,t) \, u_8(x,t)}{Pu_8(x,t)} \tag{A6}$$

$$\frac{du_7(x,t)}{dt} = s_7 - r_9 \tag{A7}$$

$$\frac{du_9(x,t)}{dt} = s_9 + r_9 \tag{A8}$$

The function s_{10} stands for water uptake by the roots, and s_6, s_7, s_8, and s_9 for ion exchange between soil solution and soil particles, and r_9 for the weathering of minerals.

APPENDIX 2. Cation Exchange Between Soil Solution and Soil Particles.

The exchange of ions between soil solution and soil particles is a dynamic process, the rate of which was assumed to be determined by the equivalent concentrations of ions in solution and on soil particles. The rates of the exchange reactions are calculated in the following equations, where cec stands for the total cation exchange capacity of the mineral soil and L for the depth. The selectivity coefficient of the Gaines–Thomas ion exchange equation is here split into the parameters v_1 and v_2.

$$s_6 = - \frac{v_1 u_9(x,t)}{cec} \left[\frac{u_6(x,t)}{u_{10}(x,t)\ L} \right]^2 + \frac{v_2 u_8(x,t)}{u_{10}(x,t)\ L} \left[\frac{u_7(x,t)}{cec} \right]^2 \qquad (A9)$$

$$s_7 = -\ s_6 \qquad (A10)$$

$$s_8 = -\ s_6 \qquad (A11)$$

$$s_9 = -\ s_6 \qquad (A12)$$

LIST OF SYMBOLS

SYMBOL	UNIT	STATE VARIABLE
Environmental variables:		
$u_1(x,t)$	$W\ m^{-2}$	irradiance
$u_2(x,t)$	$^\circ C$	temperature
$u_3(x,t)$	$g\ m^{-3}$	concentration of CO_2
$u_4(x,t)$	$g\ m^{-3}$	concentration of SO_2
$u_5(x,t)$	$g\ m^{-3}$	concentration of O_3
$u_6(x,t)$	$eq\ m^{-3}$	hydrogen ions in soil solution
$u_7(x,t)$	$eq\ m^{-3}$	hydrogen ions on exchanging surfaces
$u_8(x,t)$	$eq\ m^{-3}$	base cations in soil solution
$u_9(x,t)$	$eq\ m^{-3}$	base cations on exchanging surfaces
$u_{10}(x,t)$	$m^3\ m^{-3}$	water content of soil
Flux variables:		
$q_3(x,t)$	$g\ m^{-2}\ h^{-1}$	flux of CO_2
$q_4(x,t)$	$g\ m^{-2}\ h^{-1}$	flux of SO_2
$q_5(x,t)$	$g\ m^{-2}\ h^{-1}$	flux of O_3
$q_6(x,t)$	$g\ m^{-2}\ h^{-1}$	flux of hydrogen ions
$q_8(x,t)$	$g\ m^{-2}\ a^{-1}$	flux of base cations
$q_{10}(x,t)$	$g\ m^{-2}\ a^{-1}$	water flux
Stand variables:		
Mn	$g\ ha^{-1}$	needle mass
Mr	$kg\ ha^{-1}$	root mass
ρ_n	$kg\ m^{-3}$	needle mass distribution
ρ_r	$kg\ m^{-3}$	root mass distribution
U^P	–	relative effect of environment on photosynthesis
U^N	–	relative effect of environment on nutrient uptake
U_n^D	–	degree of damage of leaves
U_r^D	–	degree of damage of roots
P	$g\ yr^{-1}$	annual amount of photosynthesis
p	$g\ g(needle)^{-1}\ s^{-1}$	photosynthetic rate
n	$g\ g(root)^{-1}\ s^{-1}$	nutrient uptake