A CONCEPT OF FOREST ECOSYSTEM STABILITY AND OF ACID DEPOSITION AS DRIVING FORCE FOR DESTABILIZATION

B. Ulrich

Institut für Bodenkunde und Waldernährung der
Universität, D-3400 Göttingen, Büsgenweg 2

ABSTRACT

A theory is proposed which explains the acidification and alcalinization of soils, respectively, as consequence of the discoupling of the ion cycle in the ecosystem. Under the assumption that the ecosystem tends to minimize net proton production or consumption in order to keep the chemical soil state in optimal conditions for growth, the characteristic features of stable forest ecosystems showing high resilience are deduced. A sequence of ecosystem states is described; aggradation phase, stability range I (high resilience), destabilization phase I (humus disintegration), stability range II (low resilience), destabilization phase II (build up of decomposer refuge, podzolization). A continuous input of acidity exceeding the rate of base cation release by silicate weathering within the root zone forces forest ecosystems from the stability ranges into the transition states (destabilization phases). The concept of stress and strain is used to deduce how acid deposition superimposes natural stress factors and may trigger forest damages connected with climatical extremes and pests.

INTRODUCTION

Many forest soils are acid. This was accepted as a fact. In the northern hemisphere, acid forest soils have been found the more often the farer north and the higher (altitude) the location has been. Since precipitation increases with increasing altitude it was assumed that stronger soil acidification in higher altitudes is caused by stronger leaching through higher precipitation. But

B. Ulrich and J. Pankrath (eds.), Effects of Accumulation of Air Pollutants in Forest Ecosystems, 1–29.

in a soil which contains no cation acids, percolation with water or with a very diluted NaCl solution (NaCl from sea spray), being in equilibrium with the CO_2 content of air, will not cause the pH to drop below 5. This means that precipitation alone will not cause the formation and accumulation of stronger organic acids and cation acids in soils.

It was further found that acid forest soils usually carry an acid top organic layer and may show bleached A horizons as well as iron enriched B horizons. The process leading to such a soil profile was called podzolization. Many investigations showed that the vegetation plays a deciding role in podzolization, mainly by the kind of leaf litter produced. This made clear that vegetation and decomposers are involved in the process of soil acidification called podzolization. The presence and the role of organic acids in this process was clearly demonstrated, but the cause for their formation remained hidden.

In Central Europe, podzolization has been found to be related to a change from forest to heath ecosystems. The disappearance of trees has been explained by utilization of biomass by man and by grazing, prohibiting the regeneration of trees. This may not be the sole reason. What does soil acidification mean in respect to forest ecosystem stability and resilience?

ROSENQUIST (1) was one of the first who tried to compare the role of natural soil acidification and of acid deposition. He made clear that the role of acid deposition has to be weighted with natural acidification.

How can such a weighing be done? Since we consider processes acting in time, the adequate measures will be rates. Thus we have to compare rates of natural soil acidification with rates of acid deposition. No data existed a few years ago on rates of natural production of strong acids in soils.

In the following a theory, first presented in 1978 (2,3,8) is shortly outlined. This theory explains the acidification and alcalinization of soils, respectively, as consequence of the discoupling of the ion cycle within the ecosystem. Similar approaches have been proposed by DRISCOLL (4), ANDERSSON et al. (5) and SOLLINS et al. (6). The theory shows further how the internal proton production or consumption in soils can be measured and calculated (from the cation/anion balance of the storage changes in soil compartments). Corresponding experimental data are given by MATZNER et al (this volume). The theory is expanded to define aggradation phases, stability ranges of different resilience, and destabilization phases of forest ecosystems. Stability ranges were characterized by steady states, aggradation and destabilization phases (transition states) are connected with increase and decrease of storages (7).

Evolution is not limited to species, also ecosystems can pass through evolutionary stages by adjusting to changing conditions during geological periods. The stability ranges and transition states described are typical for the geological and climatical conditions of Central Europe. Under different conditions, other stability ranges can occur as a result of ecosystem evolution.

The element cycles in forest ecosystems are subjected to two general rules: the rule of continuation of mass and the principle of electrical neutrality. The last one has especially to be considered if the elements pass from one phase to another one as ions. Precondition for the application of these rules on data sets is the simultaneous measurement of the total ion turnover in the ecosystem. This is methodical difficult, but can be achieved with enough accuracy (8,9). By considering possible errors, the measuring approach can be limited to the quantitatively most important ions: all those cations and anions can be neglected whose contribution to cation sum and anion sum, respectively, is less than the error of this sum.

THE ION CYCLE IN THE ECOSYSTEM IN STEADY STATE

By defining the ecosystem in a proper way, all processes included in ion turnover can be reduced to four fluxes: input (e.g. from atmosphere, or by weathering of soil minerals), output (e.g. leaching, denitrification), uptake from soil solution into biomass (by plants and microorganisms), and release of ions during decomposition (mineralization). We consider an ecosystem in which input and output are equal for each element. For such an ecosystem, quasi-steady state can be achieved: in the temporal and spatial mean all stores in the system are constant. This covers phytomass, total biomass, soil organic matter, the various chemical elements and their various binding forms. In such an ecosystem the rate of assimilation must be equal to the rate of respiration, or, if one includes also the turnover of elements other than C, H and O, the rate of phytomass production must be equal to the rate of mineralization:

$$CO_2 + H_2O + X^+Y^- \quad \underset{\text{mineralization}}{\overset{\text{phytomass production}}{\underset{\longleftarrow}{\overset{\longrightarrow}{\text{energy}}}}} \quad CH_2OX^+Y^- + O_2$$

In eq. 1, X^+Y^- symbolyzes the cations and anions of the elements other than C, H and O; they are taken up from the soil solution and return during mineralization again to the soil solution. For the ion cycles coupled in soil, the principle of electroneutrality says that in each compartment, soil solution or plant, the cation/anion balance must be zero. If during phytomass production more anions Y^- are taken up than cations X^+ (or vice versa), the resulting charge inequilibria must be balanced. If this is not possible, ion uptake must cease. The same holds for mineralization. The charge balancing can occur by proton transfer. If anion uptake exceeds cation uptake, protons must be taken up in addition (or OH^- must be transferred from plant to soil; this can happen by transport of HCO_3^- which, by being transformed to CO_2 and H_2O, transfers one proton from the soil solution into H_2O). If cation uptake exceeds anion uptake, the proton transfer must occur in the opposite direction. If in the steady state the process of phytomass production is exactly balanced by mineralization, than the proton transfers connected with uptake and mineralization are of opposite direction and balance each other.

It is known from many investigations that the ion turnover occuring by mineralization and uptake is connected with proton production or consumption and causes changes in the pH value in the medium (for plant uptake see 10). Hitherto the single processes have been looked at, e.g. the uptake of nitrogen as ammonium or nitrate. The effect in the ecosystem,however, can be judged only if the total ion turnover is considered simultaneously, and if the ionic status (uncharged, cation, anion) in each compartment (soil solid phase, soil solution, plant) is taken into consideration (MATZNER et al. this volume). Calculations of the proton production in ecosystems which are based on single processes only and not on complete ion balances (11) are therefore meaningless.

THE ION CYCLE OF AN EVEN AGED BEECH STAND - AN EXAMPLE

The turnover rate in the ion cycle can be approached by measuring and calculating the rate of ion uptake by the vegetation. In table 1 data are given for a beech (Fagus silvatica) stand, 120 years old, on a podzolic brown earth developed within a loess layer overlying red sandstone; the site is located in Central Europe in the Solling district in 500 m altitude. The total uptake rate is calculated as the sum of transport rates in litter and canopy leaching, the accumulation rate in the incremement, and the turnover rate of fine roots.

Since the form of nitrogen uptake is unknown, the both extreme cases are considered separately:
hypothesis A: N uptake exclusively as NO_3^-
hypothesis B: N uptake exclusively as NH_4^+
From the data of table 1 it follows that the rate of cation uptake amounts to 5.29 keq, the rate of anion uptake to 1.01 keq, and the rate of N uptake to 5.80 keq. In the case of hypothesis A, N uptake occurs as anion. In this case the anion uptake amounts to 6.81 and exceeds the cation uptake by 1.52 keq. This anion surplus would have been balanced by proton uptake from soil. In the case of hypothesis B, the N uptake occurs as cation. In this case the surplus is in cation uptake and amounts to 10.08 keq; it would have to be balanced by a corresponding proton transfer from the plant into the soil.

Table 1: Ion uptake in a beech forest on podzolic brown earth in the Solling

way of turnover	Na	K	$\frac{1}{2}$ Ca	$\frac{1}{2}$ Mg	$\frac{1}{2}$ Mn	$\frac{1}{3}$ Al	$\frac{1}{3}$ Fe	Cl	$\frac{1}{2}SO_4$	H_2PO_4	N_t
						$keq \cdot ha^{-1} \cdot yr^{-1}$					
litter fall	0,03	0,41	0,81	0,13	0,19	0,00	0,07	0,02	0,28	0,13	3,5
canopy leaching	0,03	0,48	0,33	0,04	0,07	0,00	0,00	0,06	0,18	0,00	0,00
storage in forest increment	0,00	0,17	0,39	0,14	0,12	0,01	0,04	0,00	0,09	0,07	0,93
storage in stocks and roots > 5mm (increment)	0,03	0,03	0,05	0,02	0,01	0,01	0,01	n.d.	0,01	0,01	0,16
turnover of roots < 2 mm	0,04	0,14	0,29	0,19	0,03	0,60	0,38	n.d.	0,08	0,06	1,21
sum = plant uptake	0,13	1,23	1,87	0,52	0,42	0,62	0,50	0,1	0,64	0,27	5,80
sum in kg element	3,0	48	37	6,3	12	5,6	9,3		10	8,4	81
uptake in above-ground plant parts in kg element	1,4	41	31	3,8	10	0,1	2,0	2,8	7,5	6,2	62

To account for the ionic status, the precursor of the ions present in soil solution and the binding form in the plant must be known. As binding forms in the soil matrix and in the plant are assumed:

N: only organic binding forms with charge zero; fixed or exchangeable NH_4^+ in soil as well as NO_3^- in plant are neglected

Na, K, Mg, Ca, Mn, Al, Fe: as cations, the charge is balanced by inorganic or organic anions

S, P, Cl: as anions balanced by cations. This is an oversimplification in case of S (S containing amino acids), but the error introduced can be neglected for the following consideration. In case of P, the pyrophsphate bound creates dissociating OH groups during its breakdown.

With the exception of N assimilation and denitrification, the input and output of all elements occurs in ionic form. The precursor of assimilated N is uncharged N_2, the reaction products of denitrification are also uncharged compounds (N_2, N_2O).

If the N accumulated in the plants stems from N_2 (after assimilation) or soil organic N (after mineralization), its transfer to plant organic N is not connected with any net change in charge neither in soil nor in plant, that means it is not connected with any net proton transfer. It is therefore not possible to calculate net proton production in soil from NH_4/NO_3 ratio during ion uptake. In the example given in table 1, the net proton source term connected with uptake is equivalent to the difference between cation uptake (5.29 keq) and anion uptake (1.01), giving a proton production in soil of 4.28 keq $ha^{-1}yr^{-1}$.

From the point of view of the ion cycle, ion uptake is controlled by two principles:

- maintenance of electrical neutrality (cation/anion balance) in the flux
- maintenance of H^+/OH^- balance in the compartments (plant and soil)

The maintenance of H^+/OH^- balance requires that a NH_4/NO_3 ratio in uptake differing from 1 is accompanied by an equivalent net transfer of protons from soil to plant (NO_3^- surplus) or reverse (NH_4^+ surplus). If uptake and mineralization occur at the same place and time with the same rate, the proton flux connected with uptake would, under steady state conditions, be supplied by the process of mineralization. It will be discussed later that the resilience of the ecosystem is the greater the better this coupling is achieved.

Plants and soils contain buffer systems which are able to produce or consume protons without great changes in the chemical potential of the proton in the solution (pH). In the case of N transfer from charge zero in soil to charge zero in plant, the buffer systems in soil and plant counteract each other. This is demonstrated by the following reaction chain, illustrating the principle:

mineralization: $N^{o}_{org} \longrightarrow H^{+} + NO_3^{-}$

soil buffering: $\boxed{\quad}\!-K + H^{+} \longrightarrow \boxed{\quad}\!-H + K^{+}$

plant buffering: $CO_2 + H_2O + (K^{+}NO_3^{-}) \longrightarrow (K^{+}HCO_3^{-})_{comp.I} + (H^{+}NO_3^{-})_{comp.II}$

protein formation: $(H^{+}NO_3^{-}) \longrightarrow N^{o}_{org}$

In case of a surplus in the uptake by NO_3^{-}, a possible proton consumption in soil during the transfer of organic bound N from soil to plant results in the formation of basicity in the plant. As example the formation of $KHCO_3$ has been postulated, but the basicity may appear in any other compound. This means that a plant alcalinization occurs which is equivalent to the previous soil acidification. In case of a NH_4^{+} surplus (surplus exceeding NO_3^{-} uptake), a plant acidification occurs which is equivalent to the soil alcalinization due to NH_4^{+} formation ($NH_3+H^{+} \longrightarrow NH_4^{+}$). The buffer (pH-stat) operating in plants may than limit N uptake.

This seems possible especially in soils with extreme nitrification conditions: in neutral soils poor in organic matter due to an extreme high rate of nitrification (NH_4 uptake tends to zero), and in soils with acute podzolization due to an extreme low rate of nitrification (NO_3 uptake tends to zero). For both conditions, special adaptations seem to have developed during evolution (e.g. mycorrhiza).

There are several mechanisms to transfer alcalinity from plant to soil: leaf leaching of bicarbonates, accumulation of Ca salts in leafs before leaf fall, diffusion of bicarbonates from root to soil. The transfer of acidity from plant to soil seems to be limited mainly to the root. The compartmentation of the soil/root system should allow proton transfer reactions of the following type:

$$(NH_4^{+}Cl^{-})_{soil} + H_2O + (CO_2)_{plant} \rightarrow (NH_4^{+}HCO_3^{-})_{plant} + (H^{+}Cl^{-})_{soil}$$

The exudation of organic acids (R-COOH) does'nt fulfill this purpose since it is not connected with a change in the H^{+}/OH^{-} balance of the plant. Only if the organic molecule is taken up again as salt and the cation is transferred to an (insoluble) hydroxide, there would be a proton transfer from plant to soil:

$$(R\text{-}COOH)_{plant} \longrightarrow (R\text{-}COOH)_{soil}$$

soil: $R\text{-}COOH + X^{+} \longrightarrow R\text{-}COOX + H^{+}$

$$(\mathrm{R{-}COOX})_{\mathrm{soil}} \longrightarrow (\mathrm{R{-}COOX})_{\mathrm{plant}}$$

$$\text{plant:} \qquad \mathrm{R{-}COOX} + H_2O \longrightarrow \mathrm{R{-}COOH} + \mathrm{XOH}$$

The cation X must be a cation acid like Al, Mn, Fe ion species. The process may be responsible for the accumulation of cation acids, especially Al, in roots. As a consequence of this process, long living plant like trees would have to renew regularly those roots, where the accumulation occurs. This should increase the root turnover. A higher root turnover needs more photosynthates and will therefore reduce the growth of the overstory (bole increment) even if the net photosynthesis remains at the same level. This process may be therefore the main reason for the decrease in forest yield on acid soils.

From this point of view, Al toxicity in trees may be connected with the cation species X^+ existing in soil solution. If X^+ is a highly charged cation like Al^{3+}, it may be transferred from soil to plant as cationic complex $(\mathrm{R{-}COOX})^+$. By the release of X in the plant, a soluble instead of an insoluble ion species is formed.

Cell metabolism should play a major role in all of these transfer reactions, as driving force as well as providing sinks and sources for the reactants. The base cations (Ca), bound in exchangeable form in the free space, can act as an intermediate buffer system. The capacity of this buffer system is limited, but it can be regenerated by metabolic activity.

If one looks at the size of the balance as well as at the processes transferring alcalinity or acidity from plant to soil, pure nitrate nutrition should be much easier balanced by the plant than pure ammonium nutrition. Balance A (only NO_3 uptake, 1.5 keq) is much lower than balance B (only NH_4 uptake, 10 keq). Exclusive NO_3 uptake should be much easier compensated in the plant by formation and disposal of equivalent alcalinity, than exclusive NH_4 uptake by formation and disposal of equivalent acidity. This means that exclusive NH_4 uptake should limit phytomass production much more than exclusive NO_3 uptake. This may be a main reason for the low productivity of strongly acidified soils where nitrification is prohibited.

AGGRADATION PHASE

The term "aggradation phase" is used here for ecosystems in which the organic matter storage in mineral soil is increasing through accumulation of organic matter with narrow C/N ratio ($\sim$10/1). The humusform is any subtype of mull. With this phase, soil and ecosystem development starts at a freshly exposed surface of loose sedimentary rocks, e.g. after glaciation. As an example a soil may be considered where an amount of 100,000 kg organic matter per ha has been accumulated, the carbon content of organic matter = 50 %, C/N ratio = 10, CEC (cation exchange capacity) = 4 eq/kg C. The CEC indicates a production of 200 kmol H^+ha^{-1}.

The N accumulated during the aggradation phase originates in untouched ecosystems mainly from N_2 (legumes), to a small fraction from nitrate input with rain. If the nitrate input is balanced by base cations, its accumulation in the ecosystem in form of organic N is connected with a proton consumption. This proton consumption occurs in plants, but is finally transferred to the soil (e.g. by root exudation, canopy leaching, litter fall). Assuming a nitrate input of 4 kg N $ha^{-1}yr^{-1}$, it will take 700 years to balance the acidification in the soil caused by the formation of the CEC of soil organic matter. The accumulation of soil organic matter with low C/N ratio in the mineral soil need therefore not to lead to soil acidification.

A forest plantation may swing back into the aggradation phase after clear cutting, under the influence of the freshly developed herb layer providing easily decomposable litter. In such a case the aggradation phase may end already after a few years, when the forest canopy closes, the herbs are suppressed, and the microclimate is changing again. In this case, the N accumulated stems from the N mineralized in the organic top layer. If the HNO_3 formed by nitrification is transported to the A horizon and taken up there, no change in soil acidity occurs. If the uptake is suppressed, e.g. by the use of herbicides, and the nitrate leached, the soil acidifies. It is not known whether during the mineralization of the organic top layer a transfer reaction of the following type is possible:

$$2\ HNO_3 + Ca(HCO_3)_2 \longrightarrow Ca(NO_3)_2 + 2\ H_2CO_3$$

It seems probable that the microcompartmentation existing in the soil allows such a transfer of acidity from the strong nitric acid to the weak carbonic acid (which passes over into $CO_2 + H_2O$). In such a case, the uptake of nitrate from the A horizon would be connected with a proton consumption, that means with a decrease in acidity.

STABILITY WITH HIGH RESILIENCE (STABILITY RANGE I)

Till now the theory rests on two general accepted physicochemical rules and a hypothetical state of the ecosystem, the steady state. One can say that each ecosystem tends towards the steady state but will never reach it (12). If the ecosystem is not in the steady state, phytomass production and mineralization does not compensate each other and a net production or consumption of protons in the soil will usually be the consequence. The fact that the steady state can never be achieved has three reasons:

- the climate, acting as regulator and determining the aim of ecosystem development, is not constant, but exhibits statistical variations. The ecosystem as a whole should tend to follow this variations.
- elements of the ecosystem like microorganisms, plants, animals, but also structural units, have a limited life span and have to be replaced continuously. The fallout of elements of the system represents a stress.
- ion uptake and mineralization may not happen in the same microcompartment of the soil. Thus there is always spatial discoupling of the ion cycle.

The seasonal variation of climate results in the seasonal discoupling of the ion cycle. After what has been said, anticipation of nitrification ahead of nitrate uptake will cause an acidification push by the net production of HNO_3. In a humid climate, acidification pushes of this kind are mainly regulated by temperature; dryness plays a role especially as a delaying factor. Mineralization begins at 0°C, increases from 5° on and reaches its optimum at 30° (13). After the warming up of soils in spring the nitrification may start earlier than nitrate uptake, thus leading to a <u>seasonal acidification push</u>. As soon as nitrate uptake follows, the deacidification phase starts. Also the wetting of a dried soil in summer or autumn may cause a seasonal acidification push.

In stable ecosystems, temporal discouplings occur in opposite direction (e.g. proton consumption following proton production), their effects on the chemical soil state do therefore compensate in the temporal mean. Spatial discouplings are compensated by the mixing activity of soil burrowing animals. The temporal or spatial discoupling may, however, already lead to cell injury in microorganisms and roots as consequence of the appearance of toxic cation acids like Al ions. There is therefore a need to buffer a net proton production for the time interval of discoupling by basic cations. This intermediate buffering is taken over by exchangeable Ca (and Mg) (see ULRICH, this volume).

If one considers cation acid (e.g. Al) toxicity as the main factor of chemical stress in natural, untouched forest ecosystems (nutrients being well balanced), than the capacity of the cation exchange buffer existing in soil is one major factor determining the resilience of the ecosystem. Parameters of this buffer system are the cation exchange capacity (CEC in keq $ha^{-1}z^{-1}$, z = soil depth) and the percentage of exchangeable basic cations (Ca+Mg). Another major factor of resilience is the mixing activity of soil burrowing animals.

The absence of toxic cation acids allows all species of primary producers and of secondary producers (decomposers and consumers) to exist and thus to compete with each other. For the climatical and hydrological conditions given one should therefore expect

the greatest diversity, compared with ecosystems on acidified soils. The absence of toxic cation acids means further that roots tend to maximize the contact with soil material where water and nutrients are stored, and that bacteria play the dominant role in the decomposers.
A stable forest ecosystem with high resilience (stability range I) should therefore, under the conditions of Central Europe, being characterized by the following properties:

- it is composed of relatively many species, which are structured in layers
- the soil is deeply rooted, the roots are homogeniously distributed
- the decomposers are characterized by the activity of earth worms
- the soil stays throughout in the silicate (or carbonate) buffer range and shows no depth gradient in the chemical soil state
- soil organic matter is accumulated throughout the whole rooting zone, due to the activity of soil burrowing animals, the soil is of crumby structure.

Examples can be found which demonstrate that untouched forest ecosystems in Central Europe would exhibit these properties.

In the higher altitudes of the subalpine mountains it is possible that a biological depth gradient existed in soil due to frost action. This should result in the formation of an organic top layer which is colonized mainly by arthropods, whereas the mineral soil can still be characterized by earthworm activity. The biological depth gradient implies a chemical depth gradient, that is the organic top layer is more acid than the mineral soil. The climatical limitations to decomposers should thus lower the resilience of the ecosystem - forest ecosystems in higher altitudes or farer north are more easily subjected to plastic strain by climatic or man-made stress.

Even in ecosystems with the soil staying in the silicate buffer range, there is some loss of cations (mainly Ca^{2+}), accompanied by HCO_3^-. This leaching from soil is responsible for the salt content of soft groundwater. In order to keep the ecosystem stable, this loss has to be balanced by silicate weathering.
A long-lasting discoupling of the ion cycle is to be expected if, in the course of natural ecosystem development, the weatherable silicates in the root zone are exhausted. If the output (leaching) of Ca and Mg becomes larger than the input (from atmosphere and by weathering), the ecosystem passes over into a nonstationary transition state which is characterized by decreasing stores of exchangeable Ca and Mg. The soil acidifies, the chemical soil state passes over from the silicate into the cation exchange buffer range. The time span needed for this process can be estimated from the buffer capacity and the buffer

rate in the silicate buffer range of the soil. With the values given elsewhere (ULRICH, this volume), the buffer capacity amounts to 750 keq $ha^{-1}m^{-1}$ per 1 % silicate content in the soil. With the buffer rate of 0.4 kmol H^{+} $ha^{-1}yr^{-1}$ for 1 m soil depth, found by MAZZARINO (this volume) for a soil of the last interglaciation period (soil "Dasburg"), a silicate content of 1 % would last for around 2000 years. If this buffer rate is accepted as typical for the natural development of untouched ecosystems on comparable soils in an interglaciation period, it means that soils with silicate contents above 5 % would still be in the silicate buffer range or swinging between silicate and cation exchange buffer range, provided that there was no acidifying influence by man's activities.

CLIMATIC ACIDIFICATION PUSHES, PHASE OF HUMUS DISINTEGRATION (DESTABILIZATION PHASE I)

Soils in the silicate buffer range without exchangeable Al at clay surfaces buffer acidification pushes by H/Ca exchange back and forth without any drastic change in chemical soil state; even the pH value may remain almost stable. The higher the percentage of exchangeable Al in the soil, the more pH can drop during an acidification push and recover during deacidification phase. Such seasonal pH variations have been recorded for forest ecosystems (14), they are typical for soil horizons swinging between silicate and cation exchange buffer range.

Especially in the higher and cooler regions of the subalpine mountains, soil temperature in the deeper rooting zone may be so far from the optimum of mineralization that in cool, humid years residues from root decomposition rich in N may be accumulated. The increase in soil temperature in and following warm, dry years can result in a strong increase in the mineralization rate as soon as the soil layer is rewetted again. Such climate fluctuations are typical for Central and North Europe. The strong and deep reeching acidification pushes in or following warm, dry years are called climatic acidification pushes. They are thus separated from the seasonal acidification pushes which are weaker and restricted closer to soil surface. It is of fundamental ecological importance that warm, dry years are a heavy load to ecosystems not only due to water stress and dryness, but also due to climatic acidification pushes. The lower the exchangeable Ca+Mg percentage, the more often toxic cation acids may be formed during an acidification push and cause injury to decomposers (bacteria) and roots.

A very long lasting discoupling of the ion cycle should result in the loss of the organic matter which was accumulated in the whole rooting zone, including the subsoil, during the aggradation phase and which was kept on a constant level during the stability range I. This type of discoupling is called humus disintegration (3,15). The ecosystem is in a non-stationary transition state which is necessarily limited in time. The time period under question may be decades to centuries, however. Under natural conditions this process seems to be bound to strong climate changes which leads to the destruction of the forest ecosystem. Examples are the changes from interglacial to glacial periods. The destruction of the forest ecosystem by man may trigger the same process.

Humus disintegration is the consequence of the discoupling between formation and breakdown of stable soil organic matter (3). Like with lignin decomposition (20), the rate of breakdown of stable soil organic matter should increase with decreasing pH and reach a maximum at pH 4.0 to 4.5. The formation of stable soil organic matter is thought to be connected with the autolysis of bacterial cultures (16, biological humification). This process may happen during gut passage in soil animals, in faeces etc. During the autolysis, phenolic rings can be formed and polymerize to water insoluble humic acids. The polymerization of the phenolic rings should be influenced by the presence of cation acids. If cation acids like Al ions are present in solution or at clay surfaces, they can form organic complexes of a relatively low degree of polymerization, which are stable against autoxidation. Polymerization is than stopped. Thus, the newly formed organic matter is easily dispersed or water soluble. It will therefore being decomposed at a higher rate. This means that the rate of formation of stable soil organic matter is decreased, at the same time the rate of breakdown is increased. The consequence is a loss of soil organic matter.

As an example we consider the same soil as before. We assume that the total soil organic matter is mineralized, the nitrogen being nitrified. Denitrification is assumed to be zero. In such a case, there would be a proton consumption by mineralization of the Ca saturated acidic groups amounting to 200 kmol/ha. On the other hand, nitrification produces 360 kmol H^+/ha. The balance of both partial processes yields a proton production of 160 kmol H^+/ha.

If one assumes that this process takes place within 100 years, the mean annual rate would be 1.6 kmol H^+/ha. This exceeds for many soils the possible buffer rate in the silicate buffer range, thus increasing soil acidity. Existing data indicate that in the early stages of humus disintegration N rich compounds are mineralized preferably. This leads to an increase in the C/N ratio of the remaining soil organic matter. During each acidification push, the NH_4/NO_3 ratio in ion uptake will be shifted to a high nitrate surplus. This will tend to limit the uptake rate of NO_3, thus prolonging the period of discoupling. In a system not being close to steady state, the chemical reactions in soil can occur far from equilibrium. Such soils can, for example, be more acid (iron buffer range) than their final state would be (aluminium buffer range, as long as clay minerals are present).

Sustained damage to primary producers is also caused by man. Clear cutting, grazing and shifting agriculture, may result in sustained reduced primary production and, even more, in sustained reduction of understory root and overstory leaf etc. litter. It further changes the microclimate of the soil, that is the climatical conditions for the decomposers. Both effects, the reduction in litter production and the increase in soil temperature, operate in the direction of lowering organic matter stores in the mineral soil. They may thus initiate humus disintegration. The process can be started by the acidity produced (alcalinity not returned) by the discoupling of the ion cycle due to biomass utilization.

ACIDIFICATION EFFECTS OF BIOMASS UTILIZATION

In table 2 the annual uptake rates and ion balances are given for different tree compartments of the same stand as shown in table 1. The tree compartments correspond to different degrees of phytomass utilization: bole (wood + bark), bole + branches, total overstory, total overstory and understory. The cation/anion balance shows that as long as only the woody parts of the overstory are used and exported from the ecosystem, the soil acidification is in a range (0.6 kmol H^+ $ha^{-1}yr^{-1}$) which can be buffered by "better" soils by base cation release during silicate weathering. If the nitrogen rich parts are continuously exported from the ecosystem (e.g. by litter utilization, which played a role during the last centuries), soil acidification increases strongly. Even the utilization of total overstory and understory represents a realistic picture of some forest areas in Central Europe during the last centuries. All forest soils, where such utilizations have been practisized, have been strongly acidified when modern forestry started. The consequences of this acidification will be discussed later (destabilization phase II).
One should assume that all forest ecosystems in Central Europe have passed after the last glaciation period through the aggradation phase and reached the stability range I. With the exception of parent material very low in silicate content, and of shallow soils, most forest ecosystems should still be in stability range I. This is not the case. Most forest subsoils are in the cation exchange or aluminium buffer range, they show no activity of soil burrowing animals, and the roots are inhomogeneously distributed. These soils must be assumed to have passed through the phase of humus disintegration centuries or millenniums ago. It must further be assumed that in most cases this process has been initiated by biomass utilization through man.

Table 2: Annual rates of ion uptake in various tree compartments (the same stand as in table 1)

	bole	bole + branches	bole + branches + leaves	total overstory + understory
	------ keq per ha and year ------			
cation sum	0.69	0.83	2.44	4.34
anion sum	0.11	0.16	0.59	0.83
cation/anion balance	+0.58	+0.67	+1.85	+3.51

INITIATION OF HUMUS DISINTEGRATION BY ACID DEPOSITION

It seems that in Central Europe all forest ecosystems which have not been subjected to humus disintegration before, have now switched over into this phase. There is no actual reason for this than acid deposition. As discussed later, acid deposition buffered at the leaf surface is transferred to the soil close to the roots via the regulation of ion uptake (cation/anion balance). Acid deposition is therefore especially suited for acidifying the soil in the deeper rooting zone. After a reduction of exchangeable Ca, this may in combination with a climatic acidification push initiate humus disintegration and prevent the process to be stopped in a deacidification phase.

In the beginning stages of humus disintegration, the ecosystem resembles the stable ecosystem in the silicate buffer range with the exception of low pH values especially in the deeper rooting zone: the humusform can be still mull, the rooting deep reaching and being homogeneous, the soil structure crumb-like. Due to the continuous surplus of nitrification compared to nitrate uptake, tree growth may be excellent and in the shrub and herb layer plants indicating high nitrogen supply appear. The Al ions released from clay minerals are bound to soil organic matter; this reduces their toxicity. The feature typical for the process running in the deeper rooting zone is the leaching of nitrate in combination with Ca and Mg. The leaching of nitrate indicates the continuous net nitrification (i.e. formation of HNO_3) in the rooting zone. The leaching of Ca and Mg indicates the acidification, i.e. the loss of basic cations and their replacement by Mn and Al ions (i.e. cation acids). The process of humus disintegration can be stopped at any point, if the rate of proton load (HNO_3 formed exceeding HNO_3 uptake + acid deposition) becomes smaller than the rate of proton consumption by base cation release during silicate weathering. All external influences (climatic effects, changes in plant cover, biomass utilization etc.) which lower nitrification rate and increase rate of nitrate uptake will lower the rate of proton production and thus tend to stop the process. That this is reached under the influence of acid deposition is very improbable, however. Also liming may be ineffective, if not the earthworm activity is high enough to transport substantial amounts of buffering substances down to the subsoil.

Due to its long duration and the excellent growth of Al tolerant tree species, the process is very difficult to recognize and nobody is aware of its dramatic end: the change of the chemical soil state into the aluminium and iron buffer range with all of its consequences for plant growth and decomposer activity. Many stands showing fir die-back seem to be subjected to humus disintegration (17). The same seems to be the case with some forest stands in the subalpine mountains. If in the final phase the root system becomes shallow, soils may become compacted on the long run with the possible consequences of erosion and waterlogging.

At the present stage of knowledge, the best measure of humus disintegration seems to be the monitoring of net losses (surplus of output above input) of nitrate and base cations from the rooting zone. To avoid changes in the seepage due to denitrification, the measurements have to be done immediately below the rooting zone by means of suction lysimeters for collection of the percolating soil solution (18,19).

MAZZARINO (this volume) gives for soils developed after the last glaciation proton consumption rates by base cation release during silicate weathering between 0.6 and 1.1 keq $ha^{-1}yr^{-1}$ for around 1 m soil depth. The soils Spanbeck 4 and Hof 3 (each 1.1 kmol H^+) have passed through the humus disintegration phase, the soil West 1 (0.6 kmol H^+) only partially. These data indicate that during humus disintegration, the rate of silicate weathering may be increased substantially (more than doubled).

DESTABILIZATION PHASE II: BUILDUP OF A DECOMPOSER REFUGE

Soils which have passed through the phase of humus disintegration more or less completely and are staying in the cation exchange or aluminium buffer range, have lost the soil burrowing animals and tend therefore to carry through litter decomposition in a top organic layer separated from mineral soil. The lower part of top organic layer may be rooted. In this case not only leaf but also root litter contributes to its formation. The accumulation of a top organic layer means in its essence the buildup of a decomposer refuge after the mineral soil has become toxic by the presence of cation acids. It is accompanied by the loss of ground vegetation and started by the retardation of leaf litter decomposition. As a consequence, a fermentation layer (OF horizon) is forming (humusform: F-mull). If the OF increases and roots are stretching between OF and A horizon, the accumulation of a well decomposed OH horizon starts (humusform: mull-like moder).

Most dead roots seem to provide a compartment for decomposers which is free of toxins (like cation acids or water soluble phenols). Root decomposition leads therefore usually to the formation of highly polymerized humin material. The accumulation can be stopped at any stage, provided that the conditions for decomposers allow to carry through decomposition and mineralization at the same rate as litter production (reaching of a steady state). This is usually achieved after developing a full OL-OF-OH profile (humusform: moder).

Almost all of the nitrogen accumulated in the top organic layer stems from mineral soil organic N which has been transferred via plant uptake and litter fall. Its transfer was not connected with a net proton production or consumption. As in plant uptake, the acidification caused by the accumulation of the organic matter is given by its cation/anion balance. Since the anions P, S and Cl can be neglected, the acidification is equivalent to the cation accumulation. In the beginning stages of the process, the cations accumulated are mainly Ca and Mg, and the relative amount accumulated is low, resulting in cation contents of about 1 eq/kg C. If one assumes that 1/3 of the annual litter production of 3000 kg dry matter corresponding to 1500 kg C, is withdrawn from mineralization and being accumulated, the acidification rate is 0.5 keq H^+ $ha^{-1}yr^{-1}$. These conditions apply to soils where the A horizon stays in the cation exchange buffer range. As discussed in detail by **MATZNER** et al. (this volume), the acidity appears partly as soluble organic acids, which are leached from the O to the A horizon. Another part can be due to NH_4^+ uptake. Both processes become effective in the A horizon. Even a low proton production rate as the one mentioned above is thus generated in a very limited soil volume and will there exceed the buffer rate due to base cation release in silicate weathering. This means that the A horizon acidifies and may pass through the cation buffer range into the aluminium and further into the iron buffer range. This process continues as long as the accumulation of the top organic layer continues. If the A horizon reaches the Al buffer range, Al accumulation in the OH horizon starts; if it reaches the Fe buffer range, podzolization including Fe accumulation in the OH horizon starts. Parallel with the transfer of Al and Fe ions from the A into the O horizon the cation carrying capacity of the O horizon is increasing and may reach values of 2 eq/kg C (table 3).

Podzolization can be seen at the soil profile by the appearance of a greyish Ae horizon. During the last 3 decades, this has become a widespread feature in forests of Central Europe. The investigations in the Solling yielded for this stage between 1966 and 1979 mean annual rates of organic matter accumulation in the top organic layer of 1200 kg (beech) to 1500 kg (spruce) per ha. The net proton production has been calculated from the ion flux balance and shows values varying between 1.2 and 3.2 (mean: 2.2) kmol H^+ $ha^{-1}yr^{-1}$ for Fagus silvatica, and between 1.2 and 5.6

Table 3: Cation equivalent sum and its composition in needles, litter, and organic top layer (Picea abies, Solling plot F1, 1973)

	cation sum eq/kg organic d.m.	1/2 Ca	1/3 Fe	1/3 Al
		-----%	of cation	sum----
needles		33	1.1	1.3
litter		46	8	9
OL horizon	0.49	18	28	32
OF horizon	0.88	11	44	37
OH horizon	1.0	9	39	46

(mean: 3.7) for Picea abies (MATZNER et al., this volume). One can compare the amount of acidity produced during 30 years at a rate of 3 kmol H^+ $ha^{-1}yr^{-1}$ with the buffer capacity in the cation exchange buffer range. This comparison yields that the amount of acidity is sufficient to leach the base cations from a 30 cm thick soil layer containing 5 % clay, or a 7.5 cm thick soil layer containing 20 % clay. The first example corresponds to typical podzols on sandy soils, the second to the type of podzolization as it is now widespread on loamy soils in Central Europe.

The typical podzols are heath podzols which developed centuries ago under the influence of extreme strong biomass utilization on sandy soils. As the development of heath ecosystems shows (22,23), podzolization is a cyclic process, an acidification phase is followed by a deacidification phase. The acidification phase is connected with the accumulation of the organic top layer. As a consequence of the strong soil acidification, the plant cover decays, the accumulated organic matter starts to decompose, and the ecosystem passes over in the deacidification phase. In this phase other plants can immigrate and repress the vegetation which has been lead to podzolization. Such plants are very often acid tolerant grasses which do not form woody roots and are thus not subjected to accumulation of cation acids inside the plant body. A succession may develop which leads back to aluminium or even cation exchange buffer range, if weatherable silicates are still available.

Also evenaged forest plantations can exert a strong tendency for podzolization. The tendency is the higher, the less decomposable the leaf litter is. It is known that phenols diminish the decomposibility (21), it seems that the presence of this toxins in the liquid phase is the deciding factor. There exists probably a feedback mechanism: Al (cation acid) tolerant shrub and tree species often produce water soluble phenols, which are able to complex cation acids and are a tool to increase NH_4 uptake and to decrease Al toxicity. On the other hand, these phenols may be toxic to soil bacteria which are responsible for the chemical breakdown of dead organic matter. Thus, adaption to NH_4 nutrition, cation acid tolerance and low litter decomposability may often be coupled. To reach a steady state between litter production and mineralization may than require that the concentration of phenols in microcompartments of the fermentation layer falls below a treshhold level. If the canopy of an evenaged young stand of spruce or pine closes, the heavily decomposable needle litter becomes the only source for the decomposers. Soils in the Al and Fe buffer range show a low tendency to oxidize and polymerize soluble phenols, in contrary they stabilize them by the formation of metal-organic complexes with Al and Fe ions. Under these conditions a strong decrease in needle litter mineralization can occur, which leads to the accumulation of an organic top layer and a strong proton production. The adverse effects of evenaged spruce plantations on soils were discussed in Central Europe already in the 2nd and 3rd decade of this century (24,25). The expectation that the growth of Norway spruce will decline in the 2nd and 3rd tree generation did not fulfill, however, in the 4th, 5th and 6th decade of this century. It seems that the delay in the expected growth decline has an external reason, being caused by the increase in deposition of nutrients like N and Ca from air pollution.

The phase where this nutrient input stimulated tree growth in Central Europe is now passed through, and the fate of the forests is now determined to a great degree by the podzolization caused by acid precipitation.

The example of heath ecosystems shows that actual podzolization lasts only for a limited period of time. The development of evenaged coniferous plantations growing on soils in Al and Fe buffer range leads to the same conclusion. 20 to 30 years after canopy closure the canopy is opened again by eliminating trees. After having accumulated a decomposer refuge, the change in microclimate caused by the canopy opening may be sufficient to reach steady state between litter production and organic matter mineralization, and the proton production stops. On soils in the silicate or cation exchange buffer range, the elimination of a limited number of trees may be enough to reach steady state. On soils being deeply acidified to the Al and Fe buffer range, all trees may be eliminated.

In past, the development of destabilization phase II has been mainly triggered by biomass utilization. It has been the natural end of the phase of humus disintegration. Modern forestry has triggered destabilization phase II by planting even-aged dense forests with tree species which posess heavily decomposable litter. Modern forestry has such contributed to soil acidification in Central Europe. On the other hand, the theory developed allows the conclusion that under the conditions of modern forestry in Central Europe, podzolization should only occur in even-aged dense coniferous forests. The widespread existence of actual podzolization in almost all forests with an organic top layer can therefore only be due to acid deposition. As stated above there are reasons to assume that the rates of proton production connected with podzolization can be endured only for a few decades. All information available points to the fact that species with long-lived roots like trees tolerate a continuous production of cation acids in the rooted soil only for a limited period of time. For many forests in Central Europe, half of this time span may already be over.

STABILITY WITH LOW RESILIENCE: STABILITY RANGE II

As already stated, the destabilization phase II can be interrupted at any stage. As soon as the mineralization rate approaches the rate of litter production, proton production ceases and the ecosystem can again reach a quasi-steady state. The chemical soil state may then slowly pass back to the cation exchange buffer range. The rate of this recovery process depends upon the rate of proton consumption by silicate weathering (base cation release): by this process cation acids are transferred to uncharged compounds and base cations produced, so the percentage of exchangeable Ca+Mg can slowly increase. Finally a steady state may be achieved where the base cation percentage fluctuates around a mean value corresponding to the effects of climatic acidification pushes and deacidification phases.

This stability range is characterized by a much lower resilience than stability range I with the soil staying in the silicate buffer range. The missing of soil burrowing animals has the consequence that within the soil compartments develop with different chemical state: Between these compartments chemical gradients exist. Such compartments are the organic top layer and the mineral soil, the different horizons within these layers, and the interior and surface of aggregates within these horizons. In any of these compartments, the cation/anion balance is kept at zero, and the H^+/OH^- balance must be kept close to zero, in order to maintain steady state. Deviations from these requirements, caused by the processes of mineralization and uptake, must be compensated by the transport of ions from one compartment to another. Such transports can be mediated by water flow, by transport within roots, and by diffusion. The extention of roots into the organic top layer may be of great advantage to avoid spatial discoupling of proton production and proton consumption, but makes the plants susceptible to drought periods. Within the mineral soil, the roots are growing along the surface of aggregates. The humic substances formed during root decomposition are therefore accumulating at the aggregate surfaces close to the roots and are not mixed within the total soil mass. This increases considerably the risk for cation acid (Al) toxicity in case of a strong seasonal acidification push: The nitric acid forms in a very small soil volume only which is close to the roots. In this small soil volume the buffer capacity is very limited. The frequency of the formation of toxic cation acids injuring microorganisms and roots is in this stability range II therefore much greater than in stability range I.

Soils with a high rate of base cation release by silicate weathering may have been able to return during decades or centuries to the silicate buffer range. Suche ecosystems swing back to the aggradation phase and may finally return into stability range I. Only the presence of interlayer Al in the clay minerals may than remember to the acidification phase which has passed through before. For most soils which developed on sedimentary rocks, glacial deposits and wind deposits in Central Europe, however, the recovery after ceasing of humus disintegration ended in stability range II. This applies also for soils where humus disintegration ceased centuries ago, and where a forest ecosystem with beech as almost only tree species developed again (Luzulo-Fagetum). If the silicate buffer rate of these soils was not sufficient to bring the chemical soil state back to the silicate buffer range, it will also not be sufficient to buffer the additional acid entering the ecosystem as acid deposition. The present knowledge allows to state that all these soils will acidify under the influence of acid deposition. These forest ecosystems have already or will in near future switch over again into the destabilization phase II. The morphological feature are the greyish A horizons indicating podzolization.

THE SUPERIMPOSEMENT OF NATURAL STRESS AND STRAIN BY ACID DEPOSITION

LEWITT (27) introduced the concept of stress and strain, developed in physics and applied e.g. in geology, into biology. The action of a stress factor on a system results in a strain. This strain may be elastic (reversible) or plastic (irreversible). Plastic strain means that the system has changed persistent some of its properties. Plastic strain can result in invisible (latent) or in visible changes. Visible plastic strain is usually called injury.

This concept helps in realizing possible interactions of various stress factors. If the action of any stress factor results in a plastic strain, this may alter the reaction of the system on the influence of a second stress factor: the range of elastic strain may become smaller, plastic strain may begin at a lower treshhold.

Fig. 1 gives an overview about stress and strain in forest ecosystems. The strain is related to ecosystem processes, the physiological reactions of the organisms behind are not considered.

The climate is the driving force for the ecosystem. Its variability causes stress. The variability in the heat climate and

Fig. 1: Stress and strain in forest ecosystems - an overview

stress factor	causal relationship	plastic strain
CLIMATE		
heat climate		
warm	acidification push	root injury
cool	deacidification phase	recovery
humidity climate		
wet	O_2 deficiency in soil	root injury
dry	water deficiency in soil	root injury
mechanical climate		
no wind	-	-
storm, snow, ice	mechanical stress to roots and canopies	
chemical climate		
normal	low nutrient input	-
close to sea coast	NaCl salt damage	crown deformance
air pollution	manyfold	leaf injury soil acidification bark(cambium)injury crown deformance root injury damage to decomposers: destabilization
CONSUMERS		
pests		
virosis		diseases
bacteria		
fungi		wood rot
insects		feeding damages
man		
biomass utilization	diminishing nutrient stocks changing microlimate diminishing feeding source for decomposers	complex: destabilization
NATURAL FALLING OUT OF ELEMENTS OF THE ECOSYSTEM		
death of individuals	e.g. change in microclimate	non in stable ecosystems
deterioration of structural units		

in the humidity climate can cause root injury. One should assume that forest ecosystems and trees as their main components are well adapted to the stress caused by the mechanical components of the climate(wind, snow cover, ice) . Since man has changed the provenience and the species composition in most areas of Central Europe, elastic strain due to these stress factors may be reduced, and plastic strain may appear earlier, in man-made forests.

The only component of the climate which has been changed drastically during the last century is the chemical climate, its change is due to air pollution. In Central Europe the input of acidity and many chemical elements into forest ecosystems has been increased by a factor between 10 and 100. The input of nutrients like sulfur, nitrogen, calcium and magnesium has increased to such a degree that it may amount to more than half of the annual uptake of these nutrients by the trees (8).

Also pests can be looked at as stress factors. Plants being subjected to plastic strain by other stress factors can be expected to be attacked easier by pests. Damages at the outer surface of the plant (leaves, bark, roots) may allow pathogenic organisms to invade a tissue. Invisible plastic strain may influence the production of secondary plant substances which may control pathogenic organisms (28, 38, 39, 40). Changes in cell metabolism may attract insects.

Biomass utilization by man plays a role in Central Europe since 5000 years. In Germany it has lead to the destruction of forest ecosystems on large areas, to soil acidification, and it has brought into existence heath and grass ecosystems of low productivity (14). Restriction of biomass utilization in forests to timber by modern forestry has lead to the recovery of many forests. This recovery was supported by the deposition of nutrients from air pollution.

Also the natural falling out of elements of the ecosystem must be considered as a stress factor. An ecosystem can continue its existence only if the natural replacement of these elements (e.g. trees in the forest ecosystem) is possible. This would be the case if the strain caused by the falling out remains elastic.

From the concept of stress and strain it follows that we would need to know the whole stress situation in order to evaluate the effect of a special stress factor. This knowledge is not available since we do'nt know the invisible strain which air pollutants and other stress factors are causing in the ecosystem as a whole and in individual organisms. We must expect that the action of many stress factors on a low level of intensity at the same time (e.g. acidity and heavy metals) can limit the elastic strain for any other stress factor so that plastic strain occurs. It is to be expected that the visible plastic strain (injury) follows after a period of invisible plastic strain. WALLACE (29) has shown that various heavy metals behave additiv in causing

injury: concentrations below treshhold level may lead to injury in case of various heavy metals being present.
If one accepts that all stress factors may interact, the problem of finding the cause for an injury must be defined as the search for the chain of effects; that is for the sequence of strains caused by various stress factors. It seems that in forest ecosystems the effects start with damages to soil microorganisms, that is to the decomposer chain, and to the short roots including their mycorrhiza. To the plants, the damages of the decomposer chain operate indirect by discoupling the ion cycle. This causes imbalanced nutrient supply and the release of toxic cation acids like Al ions which in turn may cause root injury.

Taking into consideration the many stress factors causing root injury, one may look at root injury as a second stress and ask for the strain it causes in the plant as a whole. During the evolution, the chemical stress in the soil has forced to develop adaption strategies which allow the plant to survive after a root injury. Especially plants growing on acid soils seem to possess a high capability to cut off damaged parts of the root system and to renew those parts rapidly. It is obvious that the renewal is bound to the condition that the stress causing the injury is diminished to a level where it causes no plastic strain. Depending upon soil conditions, the recovery time may therefore vary considerably. The longer recovery needs, the stronger the strain to the plant of a root injury should be. Injury caused by toxicity of cation acids like Al ions should very much depend upon the degree of soil acidification. The more acids are accumulated in soil, and the stronger these acids are, the longer a toxic concentration level may persist in the soil solution after an acidification push. Under the conditions of deposition of heavy metals from air pollution, a further effect comes into play. Under all soil conditions these heavy metals seem to be accumulated in the roots (30), probably in the cell wall space of the long roots and of lignified roots. The accumulation of Al and heavy metals in this tissue means the accumulation of potential toxins close to living cell surfaces. If after the injury of mycorrhiza and short roots an acid soil solution can penetrate into these tissues, it can mobilize the Al and heavy metals present and transfer them into toxic cation acids as result of the buffering of protons. This will especially be the case if the Ca content in the root is already low as in strongly acidified soils (cf. ULRICH, this volume, BAUCH, this volume). It must be expected therefore that the accumulation of Al and heavy metals in roots increases the extent of root injury after it has started as consequence of an acidification push, and it prolongs the time necessary for recovery.
A plant with damaged roots may continue water uptake as long as no air enters the vessels and causes embolism. Without doubt plastic strain due to drought is increased. Therefore, if

drought is causing injury, one can nothing say about the primary cause without knowing whether there have been root damages before. If this is the case, than the primary cause of the drought damage may be the stress factor which caused the root injury.

In a plant with damaged roots, part of the water entering the xylem vessels may not have passed through living cells of the endodermis. During this passage the ionic composition of the transpiration stream is controlled. The avoidance of this passage means that the nutrient composition of the transpiration stream may become unbalanced and that even cation acids can become components of the transpiration stream. Probability and extent of these effects increase with increasing soil acidification. As a consequence different strains may develop: nutrient deficiency (especially of Mg and B), increased leaching of nutrients from leaves (strengthening nutrient deficiencies), reduced basicity transported to leaves, disturbances in cell metabolism (invisible plastic strain, reducing production of secondary plant substances, thus lowering the resistance against pathogens). A further possibility is that pathogens invade the plants through the injured roots and are transported passively with the transpiration stream inside the root system and further into other tissues. This is one link in the chain which leads to fir dye-back (31,32, 33);the primary causes of the fir dye-back are therefore the soil conditions which allow the climatic variations to cause root injury and which prevent rapid recovery. If these soil conditions are due to acid deposition, than acid deposition is the primary cause.

The same must be expected to be applicable to root rotting fungi. Since many wind-thrown trees show uncured root damages (34), acid deposition can be the primary cause for forest damage by wind-throw. This seems in fact to be the case for the heavy wind-throw occuring in November 1972 which caused forest damage to more than 100000 ha in Lower Saxony. The root damage was induced by the acidification push following the warm-dry years 1967/69, but due to soil acidification by acid deposition. The extinction of the forests having root damage by this wind-throw may be the reason that the forest damages which developed during the last years (as consequence of the acidification push induced by the warm-dry years 1975/76) have not shown up already in 1973 and 1974.

Tree leaves can buffer acidity deposited on the leaf by exchange with Ca; it is assumed that Ca is exchangeable bound on acidic groups in the cell wall and that the buffering occurs by H/Ca exchange. During stomata closure this exchange may be reversed forced by an input of $Ca(HCO_3)_2$; the carbonic acid formed may be assimilated or transferred to H_2O and CO_2:

$$\text{buffering:}\ \boxed{\begin{array}{c}\text{cell}\\ \text{wall}\end{array}}\begin{array}{l}-O^-\\ -O^-\end{array}Ca^{2+} + 2H^+ + SO_4^{2-} \rightarrow \boxed{\begin{array}{c}\text{cell}\\ \text{wall}\end{array}}\begin{array}{l}-OH\\ -OH\end{array} + \underset{\text{leached}}{Ca^{2+} + SO_4^{2-}}$$

recharching: $$\boxed{\begin{array}{c}\text{cell}\\ \text{wall}\end{array}}\begin{array}{l}\text{-OH}\\ \text{-OH}\end{array} + \underset{\substack{\text{transpiration}\\ \text{stream input}}}{Ca^{2+} + 2\ HCO_3^-} \rightarrow \boxed{\begin{array}{c}\text{cell}\\ \text{wall}\end{array}}\begin{array}{l}\text{-O}^-\\ \text{-O}^-\end{array}Ca^{2+} + H_2O + CO_2$$

If the Ca is supplied from the exchangeable pool in the soil, the amount of basicity fed in the transpiration stream is balanced by an equivalent amount of acidity formed in the soil:

soil acidification: $$\boxed{\begin{array}{c}\text{soil ex-}\\ \text{changer}\end{array}}Ca^{2+} + \underset{\substack{\text{from root}\\ \text{and decom-}\\ \text{poser respiration}}}{H_2CO_3} \rightarrow \boxed{\begin{array}{c}\text{soil ex-}\\ \text{changer}\end{array}}\begin{array}{l}\text{-H}^+\\ \text{-H}^+\end{array} + \underset{\substack{\text{input to trans-}\\ \text{piration stream}}}{Ca^{2+} + 2HCO_3^-}$$

Each living cell acts as a biochemical pH-stat. Within cells organic acids and their salts form a buffer system. To be effective outside cells, the effects of the biochemical reactions controlling pH must be transferred to the cell wall space (free space, apoplast) and through the xylem or phloem from one tissue to another. According to the pH range encountered, carbonic acid and its salts has to take over this task within the transpiration stream and the free space in roots and leaves connected with it.

Proton buffering occuring in leaves is thus immediately transferred to the soil. From a physico-chemical point of view it needs a pH around or above 5 and an appreciable amount of exchangeable Ca ions present at the acidic groups in the Free Space of the roots to charge the transpiration stream continuously with $Ca(HCO_3)_2$. Decreasing Ca content in the root indicates that the pH in the Free Space is dropping, the formation of $Ca(HCO_3)_2$ becomes limited, and the transport of basicity to the leaves is diminished. As shown elsewhere (ULRICH, this volume), the reduction of the Ca content in roots proceeds proportional to the reduction of exchangeable basic cations in the soil. This means that the pH-stat in root cells cannot maintain optimal conditions in the free space of the root. Low Ca contents and Ca/Al ratios in roots thus indicate invisible plastic strain. If after a root injury, acid soil solution containing cation acids flows directly into the transpiration stream, this acidity may balance the basicity charged in from intact roots more or less.

pH measurements in throughfall of forest canopies show that the pH in the water films covering leaf surfaces may drop to 2.75 in the monthly mean (35), which means that within episodes it may be substantial lower.

The reduction in the amount of basicity transported to the leaves should have several consequences:

- pH values below 4 and especially below 3 may, depending upon their duration, lead to cuticula erosion (36). This may increase the leaching of nutrients and decrease the resistance against drought (cuticular transpiration) and pathogens.

- There is convincing evidence (37) that cell injury by SO_2 is bound to the transport of physical dissolved SO_2 ($SO_2 \cdot H_2O$, H_2SO_3) through the cell membrane. The existence of physical dissolved SO_2 depends upon pH, the ratio of SO_{2aq} to HSO_3^- is 0.0 1 at pH 3.8 and 0.1 at pH 2.8. This means that with pH values approaching 3 within the cell wall space of the stomata, very low concentrations of SO_2 should already be enough to cause cell injury. Under conditions of low pH in throughfall (as indicator for pH in water films covering plant surfaces), SO_2 injury may occur at SO_2 concentrations of 20 $\mu g/m^3$ (WENTZEL, this volume). Direct SO_2 injury to leaves seems to be connected with many of the forest damages reported.
- As shown by MAYER (this volume), heavy metals from deposition are accumulated on leaves and bark. That means that there is a tendency for increasing concentrations of potential toxins during the life span of these plant organs. The solubility of the compounds accumulated increases with decreasing pH, at pH below 3 many of the heavy metals exist as ions (cation acids) in the solution. The longer the accumulation of these elements continues, and the weaker the buffering action of leaves and bark becomes, the greater is the probability that cation acids pass over into cells and influence cell metabolism. The lowest degree of strain should be connected with disturbances of the ion balance in the cell, especially the balance of micronutrients. This may result in disturbances of growth hormons. Such effects are in fact part of the damages which can be observed. The highest degree of strain is cell death and the formation of necrotic tissue. Also this seems to play a considerable role and may explain bark necrosis as well as necrosis at the twig base leading to premature abscission of green leaves and short twigs throughout the whole vegetation period, provided the plant surfaces are wetted. Both effects are very widespread and can be observed at many tree species. Any stage of increased leaf and twig losses and dyeback can be found in the forests, from the very beginning up to tree death. The symptoms are now occuring at trees of any age, provided they are exposed and can accumulate heavy metals from deposition. The acidity, whether direct or in form of cation acids, may also injure the aperture mechanism of the stomata and thus decrease drought resistance.

Many of the possible strains caused by root damage as stress factor are at present of hypothetical nature and need further detailed investigation. On the other hand, the possible strains mentioned rest on accepted theories and on observations and can at present not be falsified. They should therefore be accepted as building stones in a general hypothesis which includes all possibilities to explain the forest damage. Such a general hypothesis should be the guiding principle for further activities.

LITERATURE

1. Rosenquist, I.Th. (1977): Sur jord - surt vann. Ingenioerforlaget A/S, Oslo, 123 p.
2. Ulrich, B. (1980): In T.C. Hutchinson and M.Havas (eds.): Effects of Acid Precipitation on Terrestrial Ecosystems, Plenum Press New York, pp. 255-282.
3. Ulrich, B. (1981): Z.Pflanzenernähr. Bodenk. 144, 647-659
4. Driscoll, Ch.T. (1980): Chemical characterization of some dilute acidified lakes and streams in the Adirondack region of New York State. Ph.D.Thesis Cornell Univ.
5. Andersson, F.T., T. Fagerström and S.I. Nilsson (1980): see 2., pp. 319-334
6. Sollins, P., C.C. Grier, F.M. McCarison, K.Cormack and R.Royel (1980): Ecological Monographs 50, 261-285
7. Bormann, F.H. and G.E. Likens (1979): Pattern and Process in a forested ecosystem. Springer Verlag New York
8. Ulrich, B., R. Mayer und P.K. Khanna (1979): Schriften Forstl. Fak.,Univ. Göttingen 58, 291 p., Sauerländer Verlag Frankfurt
9. Matzner, E. und B. Ulrich (1981): Z.Pflanzenernähr.Bodenk. 144, 660-681
10. Nye, P.H. and P.B. Tinker (1977): Solute movement in the soil-root system. Blackwell Oxford
11. Straughan, I.R., A.A. Elseewi and A.L. Page (1981): An overview of acid deposition and its impacts on soils. Paper given at the Conference on Heavy metals in the environment, Amsterdam, Sept. 1981
12. Ulrich, B. (1981): Forstarchiv 52, 165-170
13. Alexander, M. (1961): Introduction to soil microbiology. Wiley New York
14. Ellenberg, H. (1978): Vegetation Mitteleuropas mit den Alpen. Ulmer Stuttgart
15. Ulrich, B. (1980): Forstwiss.Centralbl. 99,376-384
16. Scheffer, F. und B. Ulrich (1960): Morphologie, Biologie, Chemie und Dynamik des Humus. Enke Verlag Stuttgart
17. Ulrich, B. (1981): Forstwiss.Centralbl. 100, 228-296
18. Cole, D.W. (1958): Soil Sci.85, 293-296
19. Hetsch, W., F. Beese und B. Ulrich (1979): Z.Pflanzenernähr. Bodenk. 142, 69-85
20. Crawford, R.L. (1981): Lignin biodegradation and transformation. Wiley New York
21. Swift, M.J., O.W. Heal and J.M. Anderson (1979): Decomposition in terrestrial ecosystems. Blackwell Oxford, chapter 4.3.3
22. Gimmingham, C.A. (1972): Ecology of heathlands. Chapmann and Hall London
23. Matzner, E. and B. Ulrich (1980): Z. Pflanzenernähr.Bodenk. 143, 666-678

24. Wiedemann, E. (1923): Zuwachsrückgang und Wuchsstockungen der Fichte. Laux Tharandt
25. Kraus, G., F. Müller, G. Gärtner und H. Schanz (1939): Thar.Forstl.Jahrb. 20, 483-709
26. Ulrich, B., R. Mayer and P.K. Khanna (1980): Soil Sci. 130, 193-199
27. Levitt, J. (1980): Responses of plants to environmental stresses. II. Water, radiation, salt and other stresses. Academic Press New York
28. Lunderstädt, J. (1980): Z.Pflanzenernähr.Bodenk. 143,412-421
29. Wallace, A. (1982): Soil Sci. 133, 319-323
30. Mayer, R. und H. Heinrichs (1981): Z.Pflanzenernähr.Bodenk. 144, 637-646
31. Schütt, P. (1981): Forstwiss.Centralbl. 100, 174-179
32. Blaschke, H. (1981): Forstwiss.Centralbl. 100, 190-195
33. Brill, H., E. Bock und J. Bauch (1981): Forstwiss.Centralbl. 100, 195-206
34. Bazzigher, G. und P.Schmidt (1969): Schweiz.Zeitschr.f. Forstwesen 120, Nr. 10
35. Matzner, E., P.K. Khanna, K.J. Meiwes, M.Lindheim, J.Prenzel und B. Ulrich (1982): Elementflüsse in Waldökosystemen im Solling - Datendokumentation. Göttinger Bodenkundl.Ber.71, 1-267
36. Jacobsen, J.S. (1980): see 2., pp. 151-160
37. Spedding, D.J., I.Ziegler, R.Hampp and H.Ziegler (1980): Z.Pflanzenphysiol. 96 351-364
38. Cates, R.G. (1980): Oecologia 46, pp. 22-31
39. Haukioja, E. (1980): Oikos 35, pp. 202-213
40. Schoonhoven, L.M. (1982): Ent.exp. & appl. 31, pp. 57-69