environment, as reflected upon the phenomenon of accelerated experimental 'aging'. Its concept is based upon the very old observation that during the process of aging, a considerable shift of minerals exists from 'hard' structures towards 'soft' tissues, resulting in an increased vulnerability of brittle bones and teeth as well as in growing pathological incrustations of arteries, periarticular tissues and the crystalline lens of the eye by calcium salts (after previous degenerative changes), in some relation with the phenomenon of 'natural' aging. The 'Progeria-like syndrome' observed by Hans Selye in rats and studied in detail by Tuchweber, Selye and his coworkers, may gain importance, in view of future ecologic studies. Some theoretical and practical aspects of the proposed environmental 'G-G' test are initiated.

Acknowledgments

The Organizing Committee of the Symposium Hans Selye (Drs A. Robert, S. Szabo and Y. Taché) would like to acknowledge the financial and organizational support received from the Hans Selye Foundation. We are especially indebted to its president Mr M. Cantin and to Mme Louise Drevet-Selye. Université de Montréal also provided important support and the organizational expertise of Dr G. Plaa, vice-president was invaluable for the planning and execution of the symposium. We also thank for the hospitality and gratifying help provided by Dr Y. Gauthier, dean of the Faculté de Médecine.

We express our gratitude to companies and institutions that provided crucial financial support: Bank of Montreal, Fonds de la Recherche en Santé du Québec, Glenbrook Laboratories (Division of Sterling Drug, Inc.), Hoffmann-La Roche, Medical Research Council of Canada, C.V. Mosby Publishing Company, G.D. Searle and Company, Serono Laboratories, Smith Kline and French Laboratories, Van Nostrand Reinhold Company (Scientific and Academic Editions) and Williams & Wilkins Publishers.

The following persons also earned our sincere appreciation with their help in the organization of the symposium and processing of the material for publication: Yolande Côté, Ginette Larue, Irène Mécs and Ovid Da Silva.

'Waldsterben': Our Dying Forests – Part II

Implications of the chemical soil conditions for forest decline

E. Matzner and B. Ulrich

Institut für Bodenkunde und Waldernährung, Universität Göttingen, Büsgenweg 2, D-3400 Göttingen (Federal Republic of Germany)

Key words. Forest decay; soil acidification; predisposing stresses; incitant stresses; contributing stresses.

Introduction

The forest decline which has become evident in many parts of Central Europe is of a complex nature[42]. It cannot be attributed to a single stress factor, but must be related to the interaction of a number of stress factors of abiotic and/or biotic origin.

In order to elucidate the relationship between different stress factors and forest decline, Manion[19] has developed a concept which describes forest decline. He also mentions one characteristic phenomenon of forest decline, which is the lack of agreement between various researchers about the 'cause' of the decline and the importance of the specific stress factors involved. Each investigation attempts to find the 'cause'.

To explain processes of complex origin such as forest decline, Manion distinguishes between three groups of stresses; predisposing, inciting and contributing stresses. Predisposing stresses are long-term factors which are relatively static, or unchanging, such as climate, soil type, the genetic potential, the age of the tree and the long-term effects of air pollutants. The last point covers, in our opinion, the chronic effects of low concentrations of gaseous pollutants as well as those of long-lasting proton input into forest soils from the atmosphere or from internal production. This aspect will be discussed later. Predisposing factors put a permanent stress on the plant and weaken it in such a way that other factors can become effective.

The second group of stresses is called 'incitant'. These stresses are short in duration and may be abiotic or biotic in nature. Examples of incitants are insect defoliators, frost, drought, salt spray, and the short-term effects of high concentrations of air pollutants. They generally produce a drastic injury. The plant attempts to recover but has difficulties because of the presence of the predisposing stress. We think that the soil acidification pushes arising within the soil from favorable climatic conditions have to be added here. This factor will also be discussed later.

The third group of stresses, called 'contributing', finally begin to appear. Bark beetles, cancer fungi, root and sap rot fungi, viruses and mycoplasms produce noticeable symptoms and signs on the weakened host. These organisms are persistent and are often blamed for the condition of the hosts.

The concept given by Manion provides a framework to cover all hypotheses on forest dieback produced so far.

Soil acidification as a predisposing stress

The acidification of a soil may act as a predisposing stress for the plant in a general way by causing a reduction in nutrient availability and/or by production of toxic ions in the soil solution leading to decreased root growth and ion uptake. For some elements (e.g. Ca and Mg) shortage and toxicity in the soil are interrelated and could be enhanced by each other[39]. Predisposing stress has been characterized as a relatively constant factor effective over a long period. Because acidification of forest soils is long-lasting, resulting in detrimental changes in the chemical state of the soil, it has to be considered as a predisposing stress. Before discussing the processes that cause the input of protons in forest soils, the mechanisms, consequences and the predisposing nature of soil acidification should be discussed briefly.

The acidification of forest soils has been demonstrated by a number of investigations[6,9,54]. It is caused by the fact that the rate of proton input is higher than the rate of proton consumption by the buffering processes in the soil. The buffer mechanisms of soils, their rates and capacities are described by Ulrich[45,47] in detail.

In soils free of lime the weathering of silicates with its associated release of basic cations like Ca, Mg, Na and K is the only process that buffers protons without the production of cation acids. Cation acids like Al-ions are potential toxins to roots and decomposers. The rate of silicate weathering, and the factors determining it, are not well known. The figures available for the rate of basic cation release and the corresponding proton consumption range from 0.2 to 2 keq $\cdot$ $ha^{-1} \cdot a^{-1}$ [2,14,26,27,45]. In many soils, e.g. those in mountainous regions derived from sedimentary rocks with loess cover and the sandy soils of the flat plains, the rate of silicate weathering could be estimated to be less than 1 keq $\cdot$ $ha^{-1} \cdot a^{-1}$.

If the rate of proton buffering by silicate weathering falls short of the rate of increase of proton load, protons are buffered by reacting with the clay mineral lattice and monomeric or polymeric Al-ions are released. Thus the exchangeable cations, mainly Ca and Mg are displaced (exchange buffer range[47]). The displaced basic cations are leached, the soil becomes impoverished and the nutrient supply becomes limited (predisposing stress). As the store of exchangeable basic cations gets exhausted (base saturation $< 10\%$, pH < 4.2), the Al-ions released during the buffering reaction appear in the soil solution in increasing concentrations, thus forming a permanent stress for the root system and the ion uptake[9,13,39].

Under conditions of Al-saturated exchange sites, the concentration of Al in the soil solution depends mainly on the sulfate concentration, because sulfate is the most dominant anion. This favors the formation of Al-hydroxo-sulfates[21,34]. Under the conditions of constant proton load, the acid (H^+, Al^{3+}) concentration in the soil solution causes root damage continuously, even to acid-tolerant tree species[32], with the consequence of an increased consumption of assimilates[51] and finally a reduced wood increment. These conditions reduce the vitality of the plants and thus create a predisposing stress. The diminished saturation of the exchange sites by bases results in a loss of the ability of the soil to buffer short term acidification pushes (by the exchange of H^+ against Ca and Mg) without releasing potential toxins (Al-ions) into the soil solution.

Before the importance of acidification pushes as inciting factors is pointed out, the most significant processes that lead to the input of protons in forest soils should be discussed briefly.

Causes of acidification of forest soils

The proton input by dissociation of the weak carbonic acid only plays a role as long as the pH value is > 5. The input of strong acids into forest soils arises mainly from three processes: The deposition of acidity from the atmosphere, the accumulation or removal of biomass in or from the system, and the process called 'humus-disintegration'. A detailed description of these processes is available in reports by Ulrich[46], Ulrich and Matzner[50], Matzner and Ulrich[24] and v. Breemen et al.[5] and only a short overview will be given here.

The rate of deposition of total acidity (H^+ + cation acids: NH_4, ⅓ Fe, ⅓ Al, ½ Mn) are given for different stands in North-West Germany in the table.

The rates of deposition of total acidity represent maximum values with respect to the load of acidity affecting the system; if the deposited nitrate is taken up by organisms, this results in an equivalent consumption of protons. The deposition of nitrate is about the same as that of NH_4. If nitrate and ammonium originating from deposition are taken up at equal rates, the production of protons during ammonium uptake is balanced by the consumption of protons during nitrate uptake. Under these conditions the deposition of protons and cation acids (other than NH_4) is the only input of acidity from the atmosphere. The rates of proton deposition therefore represent only minimum values for the load of acidity.

The rates of deposition of acidity need to be compared with the rates of proton buffering by silicate weathering for soils free of lime, as stated above. The rate of proton buffering by silicate weathering is estimated to be in the range of 0.2–1 keq $\cdot$ $ha^{-1} \cdot a^{-1}$ for most forest soils for a soil depth of about 1 m. As the input of acidity occurs mostly at the soil surface, that is in a limited volume, the rates of silicate weathering will only exceptionally be high enough to keep the whole of the soil within the silicate buffer range[47]. Consequently, under the present load of acidity, soil acidification leading to buffering of protons through the release of Al or Fe (Al/Fe buffer range) can be expected in most forest ecosystems of Central Europe.

During their passage through the forest canopy the protons resulting from atmospheric deposition are buffered to a significant extent by ion exchange on the leaf and bark surfaces of the trees. The rates of this process are given in the table, and the mechanism is described in detail by Ulrich[48,49] and Matzner and Ulrich[24]. The process of buffering on the stand surfaces leads finally to an equivalent proton production during ion uptake in the soil. Consequently the buffering action of the stands does not reduce the load of acidity that affects the soil, but

Rates of deposition of total acidity and rates of proton buffering by the stand (keq $\cdot$ $ha^{-1} \cdot a^{-1}$)

Location	Göttingen	Solling		Heide		Hamburg			
Time	1981/82	1969–1981		1980/81		1981/82			
Species	Beech	Beech	Spruce	Oak	Pine	Birch/Beech	Beech	Oak/Beech	Pine
Total acid deposition	1.6	3.2	5.4	1.6	2.3	2.7	2.0	1.9	3.6
H^+-Deposition	1.0	2.0	4.0	1.0	1.3	2.0	1.3	1.2	2.5
H^+-Buffering by the stand	0.5	0.6	0.9	0.5	0.3	1.1	0.6	0.4	0.5

results in a direct load of acidity in the soil surrounding the roots. The volume of soil close to the roots is very limited and will acidify rather quickly by this process.
The proton load of the soil close to the roots is enlarged by the proton production resulting from ion uptake by the plants. Plants often take up more cations than anions (especially under conditions of reduced nitrification which are found in acid soils). In order to keep electroneutrality in the soil and within the plant, a proton flux from the root into the soil is required. (Under steady state conditions, this flux will be balanced by an equal proton consumption during the decomposition of organic matter).
The acidification of the soil close to the roots has been clearly demonstrated for agricultural crops. Schaller and Fischer[40] and Marschner and Römfeld[20] report pH gradients of more than 2 units in the rhizosphere when compared with the surrounding soil matrix. Comparable pH gradients are to be expected in slightly acidified forest soils, but investigations are still lacking.
However, the chemical analysis of tree roots indicates that the concentration of Al[37] and heavy metals[25] is usually independent of the chemical status of the soil matrix. This leads to the conclusion that the pH values of the soil surrounding roots is low continuously or for specific periods, caused by the production of protons in the rhizosphere by ion uptake and buffering of the stands.

The proton production caused by ion uptake in a stand is a significant factor when evaluating the spatial distribution of the processes acting within the soil. The proton load of the whole soil is only less affected by ion uptake and the associated proton turnover because the proton turnover caused by mineralization of organic matter, which behaves in an opposite manner to the one resulting from ion uptake, has to be taken into account[23]. A net proton load of the soil will result during the accumulation of biomass in the system or when biomass is removed from the system. Under such conditions, the production of protons by ion uptake is no longer balanced by the consumption of equivalent amounts during mineralization. The proton load of the soil as a result of this discoupling of the ion cycle increases as the nutrient content of the accumulated (or removed) biomass increases. It is rather low in the case of wood (0.2–$0.6\ \text{keq} \cdot \text{ha}^{-1} \cdot \text{a}^{-1}$) but could reach high values when litter is accumulated or removed (1–2 keq)[46]. That is why the intensified use of biomass in forest ecosystems could result in a proton load of the soil that exceeds the rate of silicate weathering and thereby induces soil acidification up to the level of Al/Fe-buffering.
Furthermore, the production of very high amounts of protons within the soil is possible by a process called 'humus disintegration'[43,46,48]. Forest ecosystems, which are nearly untouched by man's activity, with soils staying in the silicate or carbonate-buffer range, have a relatively high C and N storage in the soil which is distributed throughout the whole rooting zone. The storage of organic bound N in the soil represents a potential acid. If the N is nitrified (HNO_3-production) and the nitrate is not taken up by roots or organisms but is leached from the soil, the soil is subjected to a load of protons amounting to 1 keq H^+ per 14 kg of nitrogen leached. An N-storage of 10000 kg/ha would produce 714 keq H^+ if the N is nitrified and lost from the system by leaching.
Most forest soils, at the present time, have small reserves of organic N in the mineral soil and significant amounts of acidity (exchangeable Al) suggesting that the processes of the mineralization of organic N and C (humus disintegration) and the connected production of acidity are responsible for the acidification of these soils. This may have occurred long before significant proton inputs from deposition of air pollutants were involved. Soil acidification due to humus disintegration which is induced by biomass utilization or, today, by acid deposition, may continue for decades or even centuries.
Current humus disintegration can be recognized by the fact that the nitrate loss from the system in seepage water is higher than the nitrogen input by deposition. These conditions were found, for example, in a beech forest on limestone near Göttingen where appropriate measurements were carried out[28].
Humus disintegration seems to be caused by the accelerated degradation of high polymeric humic substances as well as by a decrease in the formation of new stable humic substances. Crawford[7] pointed out that the degradation of high polymeric phenolics by fungi shows a maximum at pH 4–4.5. When the pH of the soil shifts from the silicate buffer range (pH > 5) to the Al buffer range (pH < 4.2) the rate of degradation of high polymeric humic substances will increase. The Al ions released during soil acidification will form complexes with organic ligands. Thus the polymerization of the ligands to new stable humic substances is restricted.
During the phase of humus disintegration opposing processes could occur simultaneously in soils. Though the soil is strongly acidified, the toxicity level is generally low because most of the Al is complexed with organic substances. The nutrient supply is high (high concentrations of nitrate and of displaced cations in the soil solution). The decomposer chain may be complete, including the presence of earthworms. Because of the ample supply of nutrients the production of biomass may be higher than expected and furthermore a ground vegetation may occur which indicates a nitrogen surplus.
Humus disintegration often starts in deeper soil layers, as indicated by a decrease of the pH with increasing soil depth. A direct proof of the process is possible by soil chemical analysis (nitrate concentration in the equilibrium soil solution from deeper soil layers) and by long-term measurement of the total nitrogen balance of the system.

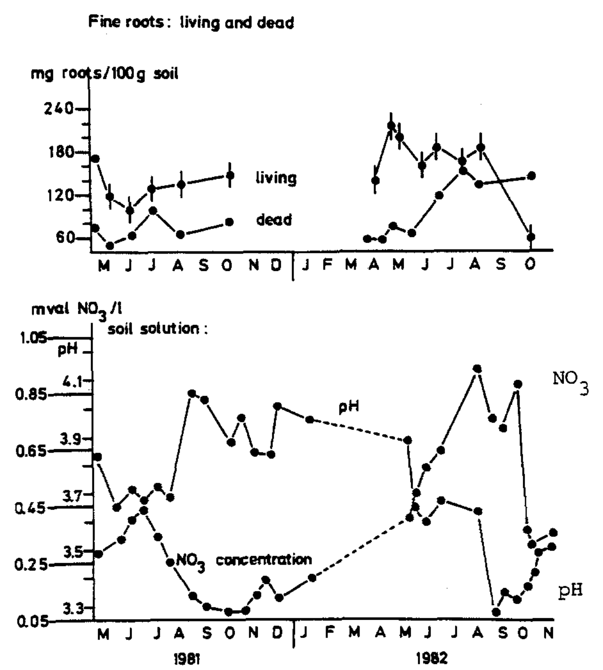
Acidification pushes as inciting stresses

The ion cycle within forest ecosystems can be condensed to two main processes: 'Mineralization' and 'ion uptake'. As stated above, both processes may be connected with proton turnover depending on the cation/anion balance of the process. If the rate of one of these processes exceeds that of the other, net production or consumption of protons may occur in the soil. The production of protons during mineralization is expected when organic N is nitrified (HNO_3 production). If the rate of nitrification exceeds the rate of nitrate uptake, protons are produced in the soil causing an 'acidification push'. The acidification push comes to an end as the nitrate is taken up by plants and microorganisms. Acidification pushes could therefore be characterized as seasonal processes related to discouplings of the ion cycle.

As it is a microbial process, the rate of nitrification is influenced by soil temperature. Normally, the mean soil temperature is far from the optimum for nitrification and a significant increase of nitrification is expected in warm years with higher soil temperature. That is why the acidification pushes are linked with warm years.

The effect of seasonal acidification pushes on soil organisms and plant roots depends on the ability of the soil to buffer the increasing amount of protons. At this point the interrelationships among acidification pushes, deposition of acidity, humus-disintegration and the accumulation of biomass becomes obvious, because the buffering capacity of the soil is being continuously stressed and slowly exhausted by the last named processes. A well-buffered soil with high base saturation is able to buffer acidification pushes by exchanging H^+ against Ca and Mg, without the occurrence of toxic ions like H, Al, Fe and Mn in the soil solution. After the soil has lost this ability, acidification pushes will more and more lead to toxic conditions in the soil.

Forest decline is generally characterized by a significant increase of the forest damage following warm and dry years. This phenomenon was first recognized in the case of the decline of *Abies* in the southern part of Germany, but also became evident in autumn and winter 1982 in many damaged spruce stands[41]. A reduction in the supply of water to trees in the warm and dry years certainly represents an additional inciting stress that may result on its own in a drastic injury to plants. The drought stress is increased if an acidification push has led to root damage, limiting the absorption power of the plant organs responsible for water uptake.



The effect of a seasonal acidification push on the dynamic of the fine roots of spruce trees in the Solling region.

The hypothesis of the occurrence and effect of acidification pushes was studied in the years 1981 and 1982 in different forest ecosystems[22]. Only the results derived from a 100-year-old spruce stand in the Solling region will be discussed at this point, because data on the dynamics of the fine roots are also available for this stand. The results of the measurements are presented in the figure; it shows the nitrate concentrations and the pH of the soil solution from the uppermost 10 cm soil depth. The data on the fine root biomass stem from 0–5 cm depth.

Already during the cool and wet season of the year 1981 the increasing nitrate concentrations (nitrification > nitrate uptake) caused a decrease of the pH of the soil solution in May. The pH value increased in autumn 1981 as a consequence of nitrate uptake (proton consumption). Again in May the nitrate concentrations of the soil solution increased in 1982 accompanied by a decrease in pH. The favorable climatic conditions in 1982 resulted in an accelerated rate of nitrification which far exceeded the rate of nitrate uptake. This acidification push resulted in a drastic decrease of the pH of the soil solution to a level of 3.28 in September 1982. The close relationship between the nitrate concentrations and pH (the H^+ and the nitrate concentrations fluctuate in equivalent amounts[22]) indicates that the upper soil of this stand no longer possesses any fast-reacting buffer characteristics. This is also evident from the only slight increase of the Al-concentration during 1982[22].

From experiments with spruce seedlings[39] it is known that roots are damaged by H^+ toxicity when the pH of the soil solution is less than 3.5. That is why the acidification push in 1982 would be expected to result in a tremendous stress on the roots of the horizon considered.

The dynamics of the biomass of the living fine roots followed the changes in solution chemistry. The amount of living roots was reduced in May 1981 as the pH of the soil solution dropped and recovered as the pH increased. Again in May 1982, the root biomass was reduced slightly, but as a consequence of the acidification push and the increased toxicity the root biomass dropped in October 1982 to the lowest value recorded during the investigation.

The data clearly show the occurrence of inciting stress to the root system arising from a seasonal acidification push in this stand, and emphasize the importance of the chemical soil conditions for the resilience of the ecosystem.

Soil chemical parameters as criteria for evaluating the implication of the soil in forest decline

Summing up the aspects mentioned above, one can conclude that the chemical stress acting in the soil changes in time and space. Spatial patterns arise from vertical chemical gradients within the soil profile as well as from gradients close to roots, around stems of trees receiving substantial amounts of acid stem flow[12,47] and in the case of a disproportionate distribution of lime (e.g. in form of stones) in the soil. Temporal patterns have been shown to arise from seasonal acidification pushes and deacidification phases. These temporal and spatial patterns make it difficult to prove the involvement of the soil conditions in the decline of a specific forest stand.

The research approach of following these temporal and spatial patterns requires the direct measurement of ecosystem processes operative in the soil by following the chemistry of the soil solution[22], root dynamics[32], and the pH of the soil close to the roots[40]. The methods to realize this approach have been developed during the last years. The research needs long-term field measurements and is therefore very expensive. The difficulties of evaluating the implication of soil-induced root injury for forest decline has led to the neglect of this predisposing stress. The present situation is that the processes have been described, and the methods to analyze the processes have been developed but are not yet in widespread use.

As a rule, one is therefore confronted with the problem of evaluating the involvement of the soil without following the processes in detail. One is then forced to draw conclusions from a 'snapshot' of the chain of events; soil acidification – acidification push – root damage by toxicity. The interpretation of such 'snapshots' will always be rather insecure and can neither prove nor disprove the chain of events.

The following soil chemical parameters could be used to evaluate the stress resulting from the chemical soil conditions: The base saturation of the exchangeable cations, the Ca/H and the Ca/Al ratios in the soil solution, and, as easily measurable parameters, the pH in water and in salt suspension. Rost-Siebert[39] pointed out that the ratio of Ca/H and Ca/Al in the soil solution gives more precise information on the risk on Al-toxicity than does the H- and Al-concentration alone. Root elongation decreases and root injury increases with decreasing Ca/H and Ca/Al ratios. Damage to spruce roots is likely if the molar ratio of Ca/Al in the soil solution is less than 1, where Al is assumed to be present as Al^{3+} ions. At values less than 0.1 severe damage to the existing fine roots can be expected. As the species of Al (monomeric, polymeric) in the soil solution strongly depend on the pH[33], these ratios can only be reached at pH values less than 4.2.

The pH of the soil solution measured in KCl indicates the pH value that may be found in the soil following a strong acidification push. The pH (KCl) also reflects the base saturation of the exchange sites. The higher the base saturation the lower is the risk of toxic conditions during acidification pushes. Base cation saturation degrees of more than 15% should normally guarantee the buffering of acidification pushes without reaching toxic levels of Al[38].

Contradictory findings like high base saturation and low pH indicate a present disequilibrium which might originate from a strong acidification push at the time of measurement. Nitrate analysis of the equilibrium soil solution could be used to elucidate these processes.

To sum up, the chemical state of the soil implies the risk of soil borne toxicity to tree roots when the pH (KCl) is less than 4.2 (possibility of toxic conditions during acidification pushes, low base saturation) and when the molar Ca/Al ratio of the soil solution is less than 1.

Plant roots can be considered as cation exchangers[8]. That is why the risk of root damage due to unfavorable soil conditions will also depend on the buffer capacity of the root. The buffer capacity of the root is characterized by the same parameters as the exchange buffer system of the soil; the higher the base saturation (Ca/Al ratio), the higher is the buffer capacity and the lower is the risk of root damage by soil borne toxicity.

Discussion

Soil acidification has been shown to act as a predisposing stress, and acidification pushes as an inciting stress for many forest stands in Central Europe. However, this does not mean that the effects of other stress factors involved in forest decline can be neglected. The existing differences in site conditions, in biotic and abiotic stresses including direct effects of gaseous air pollutants and of airborne acidity, and the differing tree responses will result in a broad pattern of effects, where the importance of particular stresses will vary.

The discussion of the importance of the chemical status of the soil with respect to forest decline has given rise to much controversy. According to Rehfuess[36], Zöttl and Mies[56], and Zech and Popp[53], the contribution of soil factors to forest decline is associated with the loss of Ca and Mg from the soil by leaching, causing a reduction in the supply of these elements to forests; the toxic effects arising from soil acidification (mainly Al-toxicity) are assumed to be improbable. Zöttl[55] denies the influence of Al-toxicity in forest decline. The origin of the widespread symptoms of Mg-deficiency, which they blame for the forest decline, has been attributed to the increased leaching of this element and of Ca and Zn from the needle tissue, caused by the direct attack of gases and acid droplets.

In recent investigations[13,39] toxic effects of Al to tree roots have been demonstrated under chemical conditions comparable to those found in the field. These and other investigations[9] have shown that the presence of Al^{3+} in the soil solution inhibits the uptake of Ca and of Mg. The observed deficiency of Ca and Mg could also be explained by the effect of Al on the roots. Bauch and Schröder[3] report from cellular analysis of fine roots of damaged and healthy fir and spruce trees that Mg and Ca deficiency in roots is always associated with fine root damage. The observation of Mg and Ca deficiency in fine roots emphasizes the reduced ability of the root system to take up Ca and Mg. The leaching of Ca and Mg from leaves is a constant process, which is generated by the acidity deposited on the leaves[44,49]. This leaching becomes a serious problem to the tree if the uptake of these elements becomes limited by Al-saturation in the apoplast of the root or by root injury in an acid soil.

Root damage is a widespread symptom in damaged stands[3,4,37,43]. There are two alternative cause/effect relationships which could explain the root damage. One is acid toxicity, as discussed above. Schütt et al.[43] and Wentzel[52] as well as Prinz et al.[35], Mohr[31] and Lichtenthaler[18] see the primary cause of the decline in the direct action of air pollutants on the leaves of the plant; the observed root damage is explained by a reduced supply of assimilates to the root system. However, as far as we know, no experimental data on that are available from damaged stands. The reduction of root growth by long-lasting fumigation of spruce seedling with 260 µg SO_2/m^3 air was shown by Keller[15] and was attributed to the deficiency of assimilates. But the concentrations used in his experiment were 5–10 times higher than those found in remote forest areas. Furthermore, it is not clear whether the root damage induced by deficiency of assimilates corresponds morphologically with that found in damaged forests. Root dieback does not only occur in damaged mature stands but is also often found in tree seedlings. The deficiency of assimilates as a primary cause of the necrotic root dieback of tree seedlings is rather improbable, especially as the root damage disappears after liming, and because the root damage is already obvious before the cotyledons appear[11,30]. In such cases, soil borne toxicity should be responsible for the root damage.

If the hypothesis is valid that the root damage is induced by deficiency of assimilates, one would expect a reduction of the fine root biomass ahead of the reduction of the wood increment. However, our investigations[51] (in connection with Athari[1]) have shown that this is not the case; irrespective of the reduction of the wood increment the trees maintain a fine root biomass of around 3000 kg/ha. Only trees with needle losses above 50% showed a reduced fine root biomass. This is not unexpected; it shows that the allocation of photosynthates to a growing (regenerating) root system is preferred. This conclusion is in agreement with earlier observations that under adverse site conditions the wood increment is reduced in favor of root growth[10,16,17,29]. The reduction of photosynthesis produced by needle losses and eventually by a reduced efficiency of the photosynthetic process, caused by direct action of air pollutants, is a serious stress to the tree. It is, however, not the only one, but is accompanied by the stress caused by soil acidity and acidification pushes.

1 Athari, S., Zuwachsvergleich von Fichten mit unterschiedlich starken Schadsymptomen. Allg. Forstz. *38* (1983) 653–655.
2 Bache, B. W., The implications of rock weathering for acid neutralization, in: Ecological Effects of Acid Precipitation. Swedish National Environment Protection Board, Report snv pm (1982) 1636.
3 Bauch, J., and Schröder, W., Zellulärer Nachweis einiger Elemente in den Feinwurzeln gesunder und erkrankter Tannen (Abies alba Mill.) und Fichten (Picea abies). Forstwiss. Zentbl. *101* (1982) 285–294.
4 Blaschke, H., Veränderungen bei der Feinwurzelentwicklung in Weisstannenbeständen. Forstwiss. Zentbl. *100* (1981) 190–195.
5 van Breemen, N., Mulder, J., and Driscoll, C. T., Acidification and alcalinization of soils. Plant Soil *75* (1983) 283–308.
6 Butzke, H., Versauern unsere Wälder? Erste Ergebnisse der Überprüfung 20 Jahre alter pH Wert Messungen in Waldböden Nordrhein-Westfalens. Forst- Holzwirt *36* (1981) 542–548.
7 Crawford, R. L., Lignin biodegradation and transformation. Wiley, New York 1981.
8 Crooke, W. M., The measurement of the cation-exchange capacity of plant roots. Plant Soil *21* (1964) 43–47.
9 Evers, F.-H., Ein Versuch zur Aluminium-Toxizität bei Fichte. Forst- Holzwirt *38* (1983) 305–307.
10 Fiedler, H. J., Hunger, W., and Zant, R., Untersuchungen über die Bodendurchwurzelung der Fichte. Archiv Forstw. (1963) 1214–1223.
11 Gehrmann, J., Untersuchungen zum Wachstum von Buchenkeimlingen in Luzulo-Fageten und Möglichkeiten ihrer Förderung durch Bodenmelioration. Allg. Forstz. *38* (1983) 689–692.
12 Glatzel, G., Sonderegger, E., Kazda, M., and Puxbaum, H., Bodenveränderungen durch schadstoffangereicherte Stammablaufniederschläge in Buchenbeständen des Wienerwaldes. Allg. Forstz. *38* (1983) 693–694.
13 Hüttermann, A., Auswirkungen 'saurer Deposition' auf die Physiologie des Wurzelraums von Waldökosystemen. Allg. Forstz. *38* (1983) 663–664.
14 Johnson, N. M., Driscoll, Ch. T., Eaton, J. S., Likens, G. E., and McDowell, W. H., 'Acid rain', dissolved aluminum and chemical weathering at the Hubbard Brook Experimental Forest, New Hampshire. Geochim. cosmochim. Acta *45* (1981) 1421–1437.
15 Keller, T., Der Einfluss langdauernder SO_2-Begasung auf das Wurzelwachstum der Fichte. Schweiz. Z. Forstwes. *130* (1979) 429–435.
16 Keyes, M., R., and Grier, Ch. C., Above- and below-ground net production in 40 year old Douglas fir stands on low and high productivity sites. Can. J. Forest Res. *11* (1981) 559–605.
17 Krauss, G. A., and Wobst, W., Über die standörtlichen Ursachen waldbaulicher Schwierigkeiten im vogtländischen Schiefergebirge. Tharandt. forstl. Jb. *86* (1935) 169–246.
18 Lichtenthaler, H. K., und Buschmann, C., Beziehungen zwischen Photosynthese und Baumsterben. Allg. Forstz. *39* (1984) 12–16.
19 Manion, P. D., Tree disease concepts. Prentice Hall Inc., 1981.
20 Marschner, H., and Römfeld, V., In vivo measurements of root-induced pH changes at the soil root interface: Effect of plant species and nitrogen source. Z. PflPhysiol. (1983) 241–251.
21 Matzner, E., Khanna, P. K., Meiwes, K. J., Lindheim, M., Prenzel, J., and Ulrich, B., Elementflüsse in Waldökosystemen im Solling – Datendokumentation –. Gött. Bodenkdl. Ber. *71* (1982) 1–267.
22 Matzner, E., and Thoma, E., Auswirkungen eines saisonalen Versauerungsschubes im Sommer/Herbst 1982 auf den chemischen Bodenzustand verschiedener Waldökosysteme. Allg. Forstz. *38* (1983) 677–682.
23 Matzner, E., and Ulrich, B., The turnover of protons by mineralization and ion uptake in a beech (Fagus silv.) and a Norway spruce ecosystem, in: Effects of accumulation of air pollutants in forest ecosystems, pp. 93–103. Eds B. Ulrich and J. Pankrath. D. Reidel Publ. Comp., Dordrecht 1983.
24 Matzner, E., and Ulrich, B., Raten der Deposition der internen Produktion und des Umsatzes von Protonen in zwei Waldökosystemen. Z. PflErnähr. Bodenk., in press (1984).
25 Mayer, R., and Heinrichs, H., Gehalte von Baumwurzeln an chemischen Elementen einschliesslich Schwermetallen aus Luftverunreinigungen. Z. PflErnähr. Bodenkd. *144* (1981) 637–646.
26 Mazzarino, M., Holozäne Silikatverwitterung in mitteldeutschen Waldböden aus Löss. Diss. Göttingen 1981.
27 Mazzarino, M., Heinrichs, H., and Fölster, H., Holocene versus accelerated actual proton consumption in German forest soils, in: Effects of accumulation of air pollutants in forest ecosystems, pp. 113–123. Eds B. Ulrich and J. Pankrath. D. Reidel Publ. Comp., Dordrecht 1983.
28 Meiwes, K. J., Charakterisierung des chemischen Bodenzustands von Böden auf Kalkgestein. Mitt. dt. bodenkdl. Ges. *38* (1983) 257–262.
29 Meyer, F. H., Gefügewandel der Mykorrhiza deutscher Waldbäume als Folge von Abwandlungen des Bodenmilieus. Forschungserg. z. Förderung d. forst. Erzeugung III, pp. 24–62. Hiltrup b. München 1961.
30 Möhring, K., Erfahren wir die Antwort der Natur? Forstarchiv *53* (1982) 123–128.
31 Mohr, H., Zur Faktorenanalyse des 'Baumsterbens' – Bemerkungen eines Pflanzenphysiologen. Allg. Forst- Jagdztg *154* (1983) 105–110.
32 Murach, D., Die Reaktion von Fichtenfeinwurzeln auf zunehmende Bodenversauerung. Allg. Forstz. *38* (1983) 683–686.
33 Nair, V. D., Aluminium species in soil solution. Göttinger Bodenkdl. Ber. *52* (1978) 1–122.
34 Prenzel, J., A mechanism for storage and retrieval of acid in acid soils, in: Effects of accumulation of air pollutants in forest ecosystems, pp. 157–170. Eds B. Ulrich and J. Pankrath. D. Reidel Publ. Comp., Dordrecht 1983.
35 Prinz, B., Krause, G. H. M., and Stratmann, H., Waldschäden in der Bundesrepublik Deutschland. LIS Berichte 28, Landesanstalt für Immissionsschutz, Essen 1982.
36 Rehfuess, K. E., Walderkrankungen und Immissionen – eine Zwischenbilanz. Allg. Forstz. *38* (1983) 601–610.
37 Reiter, H., Alcubilla, M., and Rehfuess, K. E., Standortliche Studien zum Tannensterben: Ausbildung und Mineralstoffgehalte der Wurzeln von Weisstannen (Abies alba Mill.) in Abhängigkeit vom Gesundheitszustand und Boden. Allg. Forstz. *154* (1983) 82–92.
38 Reuss, J. O., Implications of the calcium-aluminium exchange system for the effect of acid precipitation on soils. J. Envir. Qual. *12* (1983) 591–595.
39 Rost-Siebert, K., Aluminium-Toxizität und -Toleranz an Keimpflanzen von Fichte (Picea abies Karst.) und Buche (Fagus silvatica L.). Allg. Forstz. *38* (1983) 686–689.
40 Schaller, G., and Fischer, W. R., pH-Änderungen an der Rhizosphäre von Mais- und Erdnusspflanzen. Z. PflErnähr. Bodenkd., in press (1984).
41 Schröter, H., Krankheitsentwicklung von Tannen und Fichten auf Beobachtungsflächen der FVA in Baden-Württemberg. Allg. Forstz. *38* (1983) 648–649.
42 Schütt, P., Das Tannensterben. Der Stand unseres Wissens über eine

aktuelle und gefährliche Komplex-Krankheit der Weisstanne (Abies alba Mill.). Forstwiss. Zentbl. *96* (1977) 177-186.
43 Schütt, P., Blaschke, H., Hoque, E., Koch, W., Lang, K.J., and Schuck, H.J., Erste Ergebnisse einer botanischen Inventur des 'Fichtensterbens'. Forstwiss. Zentbl. *102* (1983) 158-166.
44 Ulrich, B., Mayer, R., and Khanna, P.K., Die Deposition von Luftverunreinigungen und ihre Auswirkungen in Waldökosystemen im Solling. Schriften aus der Forstl. Fak. d. Univ. Göttingen, Bd. 58 (1979) 1-291.
45 Ulrich, B., Ökologische Gruppierung von Böden nach ihrem chemischen Bodenzustand. Z. PflErnähr. Bodenkd. *144* (1981) 289-305.
46 Ulrich, B., Theoretische Betrachtung des Ionenkreislaufs in Waldökosystemen. Z. PflErnähr. Bodenkd. *144* (1981a) 647-659.
47 Ulrich, B., Soil acidity and its relations to acid deposition, in: Effects of accumulation of air pollutants in forest ecosystems, pp. 33-45. Eds B. Ulrich and J. Pankrath. D. Reidel Publ. Comp., Dordrecht 1983a.
48 Ulrich, B., A concept of forest ecosystem stability and of acid deposition as driving force for destabilization, in: ref. 47, (1983b) 1-29.
49 Ulrich, B., Interaction of forest canopies with atmospheric constituents: SO_2, alcali and earth alcali cations and chloride, in: ref. 47, (1983c) 33-46.
50 Ulrich, B., und Matzner, E., Abiotische Folgewirkungen der weiträumigen Ausbreitung von Luftverunreinigungen. Forschungsbericht 104 02615. UBA, Berlin 1983.
51 Ulrich, B., Murach, D., and Pirouzpanah, D., Beziehungen zwischen Bodenversauerung und Wurzelentwicklung von Fichten mit unterschiedlich starken Schadsymptomen. Forstarchiv *55* (1984) 127-133.
52 Wentzel, K.-F., Waldbauliche Erfahrungen zur Erkennung der Immissionswirkungsmechanismen. Allg. Forst- Jagdztg *154* (1983) 181-185.
53 Zech, W., und Popp, E., Magnesiummangel, einer der Gründe für das Fichten- und Tannensterben in NO-Bayern. Forstwiss. Zentbl. *102* (1983) 50-55.
54 v. Zezschwitz, E., Akute Bodenversauerung in den Kammlagen des Rothaargebirges. Forst- Holzwirt *37* (1982) 275-276.
55 Zöttl, H.W., Zur Frage der toxischen Wirkung von Aluminium auf Pflanzen. Allg. Forstz. *38* (1983) 206-208.
56 Zöttl, H.W, und Mies, E., Die Fichtenerkrankung in Hochlagen des Südschwarzwaldes. Allg. Forst- Jagdztg *154* (1983) 110-114.

0014-4754/85/050578-07$1.50 + 0.20/0

The effects of acid deposition on the physiology of the forest ecosystem

A. Hüttermann

Forstbotanisches Institut der Universität Göttingen, Büsgenweg 2, D-3400 Göttingen (Federal Republic of Germany)

Key words. Acid deposition; Al-toxicity; Ca/Al antagonism.

Introduction

Although there is much disagreement about the causes of the 'disease', there is one point about which almost all authors publishing on it are in full agreement: the forests in Germany are in danger of dying of a 'new' disease, which is spreading rather dramatically[47]. In addition, there is disagreement about the scientific approach which should be used to evaluate the factors (causal agents, combination of stresses, etc.) which may be responsible for the observed dieback in German forests.

The approach taken by Ulrich[45] is the analytical one laid down by Popper[40]. According to Popper, the pathway to scientific knowledge consists of three main steps. The first is the establishment of a hypothesis, based on measurements and observations. In the second step, one attempts to falsify this initial hypothesis with subsequent measurements and observations. In the last and decisive step the hypothesis becomes an accepted theory, if all attempts fail to falsify it. The same approach was used by Mohr earlier in describing how biological sciences acquire scientific knowledge[37].

Since we are dealing with a rapidly progressing disease, it might also be appropriate to apply Koch's postulates. In his classical paper of 1884, he elaborated the following requirements for the proof of the cause of an infectious disease[32]:

1) The infecting agent must be present in all patients showing symptoms of the disease.
2) The infecting agent must be isolated from the patient.
3) It must produce the disease under controlled conditions in the laboratory.

Applying these well-established criteria to the disease in the German forests, and using new information from plant physiology, biochemistry, and clinical diagnostics, the following conclusions are evident[21]: before any infectious factor, agent, substance, substance combination, etc. can be considered seriously as a possible main cause of the forest dieback, the following minimal requirements must be met.

1) It must be shown to be present in wide areas in Germany and elsewhere where forest dieback has been observed.
2) Controlled exposure of trees to the suspected causal agent under conditions and in amounts occurring in the forest must reproduce the observed symptoms.
3) An elimination of this factor in the forest must be accompanied by a relief of the symptoms.
4) In laboratory experiments, criteria should be established for a diagnosis of this factor which should be as precise and specific as technically feasible.
5) The action of the factor should be demonstrated in the declining forests on the basis of the established differential diagnosis.
6) The mechanism of action of the substance should be elucidated and the observed symptoms should be explainable on the basis of the proposed mechanism.
7) If a primary role is to be assumed, the specificity of action of the factor in question must be demonstrated. In addition, it must be possible to exclude other possible factors as major causes of the disease.

It is apparent, however, that the effects of the causal factors may not be as simple as those, for example, of virulent bacteria such as *Vibrio cholerae* or *Mycotobacter*