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

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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*

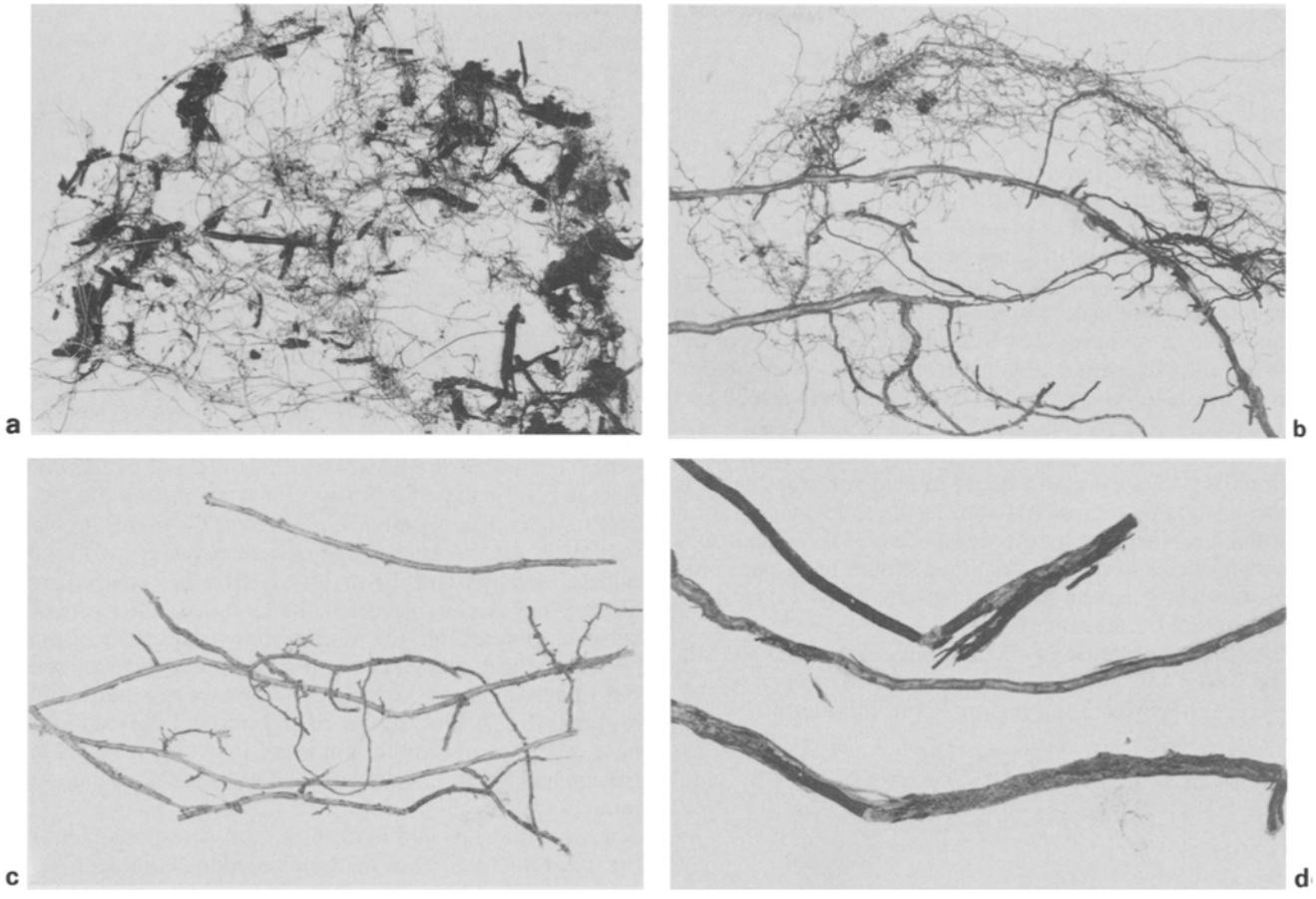

Figure 1. Morphology of roots taken from different soil horizons of a soil subjected to acid deposition. Stand: Niederkrüchten, Abt. 10, Forstamt Mönchengladbach, NRW; brown earth showing signs of podsolation. *a* Roots from the OH-layer (F-horizon), pH_{H_2O} 4.09, pH_{KCl} 3.01. *b* Roots from the Ae-horizon (0–7 cm), pH_{H_2O} 3.98, pH_{KCl} 2.88. *c* Roots from the Bsh/Bv-horizon (7–50 cm), pH_{H_2O} 3.88, pH_{KCl} 3.11. *d* Roots from the Cv-horizon (below 50 cm), pH_{H_2O} 4.38, pH_{KCl} 4.18.

tuberculosis. In addition, we should keep in mind that even if a biotic phytopathogen is identified in declining forests, this may not mean that this is the initial factor responsible for the decline. This has been shown by Falck[9,10], and the concept of decline diseases has again been summarized by Manion[34]. The fact that the situation in an ecosystem is very complicated compared with a simple infectious disease, however, does not free us from the requirements of Koch's postulates by any means. These are the minimal scientific standards one has to meet to be taken seriously in one's scientific approach. Research on the decline diseases of Central European forests is much too young in general to be able to meet all these requirements for all the factors discussed. In this paper, however, we would like to make the attempt to use Koch's postulates for the evaluation of one factor which seems to be responsible for at least part of the damage which we observe at present in northern Germany, namely soil acidification.

Causes of soil acidification

If all emissions which produce acid (SO_2 and NO_x) are summarized[47], and it is assumed that about the same amount eventually reaches the vegetation in the form of acid deposition, then the average acid deposition caused by air pollution should be in the range of about 6 kmoles protons $h^{-1}a^{-1}$. The actual values, however, vary considerably between 5.4 keq $H^+ha^{-1}a^{-1}$ in a spruce forest in the Solling and 1.6 in a beech forest in Göttingen[24]. These data, mean values of long-term observations by Ulrich and his coworkers, very probably reflect the range of actual acid deposition in Germany. Although the situation is more complicated than these rather simple figures suggest[24], it can be taken for granted that the actual acid deposition will in most cases far exceed the rate of proton consumption during silicate weathering[2,46].

An additional source of acid formation inside the soil is the humus disintegration[35,44]. It can be summarized as follows: in soils which have been subjected to the influence of acid deposition, the normally balanced relationship between the rate of humus disintegration and repolymerization is disturbed in such a way that the disintegration occurs as usual but repolymerization to humic acids is inhibited by metal-chelation of the monomers, rendering them less accessible to the action of the phenol oxidases. This process leads to an increase of nitrogen mineralization and subsequently to a nitrate surplus, especially in warm dry years[24,45].

In summary, it is altogether obvious that soil acidification is a process which has inevitably changed the properties of a wide range of soils in Germany during the last decades[6]. These changes are manifest in the biology of the soils as well[19,22].

Action of soil acidification on roots

If the root system of trees in soils which have been subjected to the influence of acid deposition are examined macroscopically, it becomes rather obvious that the root system changes dramatically with increasing depth of the soil (fig. 1). The best development of fine roots can be observed in the top soil and in the A_h-horizon which still has a higher content of organic (= humic) substances. In the mineral soil, in soil depths below 20 cm, no development of fine roots takes place in such acid soils. This is exactly the opposite situation from that which can be observed in orchards which are fertilized and where the pH of the soil is much higher. Here the highest number of root tips is to be observed in soil depths between 20 and 140 cm[49].

The explanation suggested by Ulrich[44] for this decline in fine roots of spruce and beech in acid soil was that it is due to the presence of Al^{3+} ions in the soil water solution which are liberated by the weathering of the silicate and clay minerals in the soil. Al^{3+} ions should be present only in soils which have a pH-value lower than 4.2, i.e. in the aluminium buffer range[46].

Careful examination of the anatomy of the fine roots in the lower soil horizons always revealed a very typical picture; necrosis in the region of the endodermis, which in extreme cases went so far that the central cylinder was more or less completely disconnected from the root cortex[20]. Therefore experiments were designed to test this hypothesis and find out whether similar symptoms could be reproduced in the laboratory. The results were rather clear; only with pH-values below 4.2 and with aluminium present in the nutrient solution were the same symptoms observed with spruce seedlings grown in hydrocultures; necrosis in the endodermis region and, in addition, in the apical meristem[43].

Another very important set of experiments for the elucidation of the influence of acid deposition on the conditions of the soil was conducted by Gehrmann[15,16]. He studied the influence of soil conditions on the growth and morphology of beech seedlings in areas where natural regeneration of beech had failed previously[5]. In his experiments, most of the beech seedlings planted in the unchanged soil (variant 0 in fig. 2) died off during the second summer after germination, whereas the plants grown in plots where the top soil had either been mixed with the mineral soil (variant B) or limed (BK) or replaced by nursery soil used by gardeners had a much better rate of survival. In addition, the morphology of the roots of the beech seedlings grown in the four different types of soil but under the same climatic conditions was remarkedly different (fig. 2). Only in the treated soils did the seedlings have a chance to develop a normal tap root, whereas in the unchanged soil, the roots died off after reaching the mineral soil.

The view that the acid load of the soil is responsible for the different survival of the beech seedlings in the differently treated soils of the experiment mentioned above is supported by a completely different observation made in stands where dieback has not proceeded so far that all natural regeneration of the beech seedlings has already ceased. In this area the process proceeds from the stem base of dominating trees (fig. 3), where the highest rate of precipitation and thus acid deposition takes place[17,18] (for details of this study see Hüttermann and Gehrmann[22] and Hüttermann et al.[23]).

From these and other experiments, we believe that the first three postulates discussed in the introduction can be considered to be fulfilled as closely as possible for the

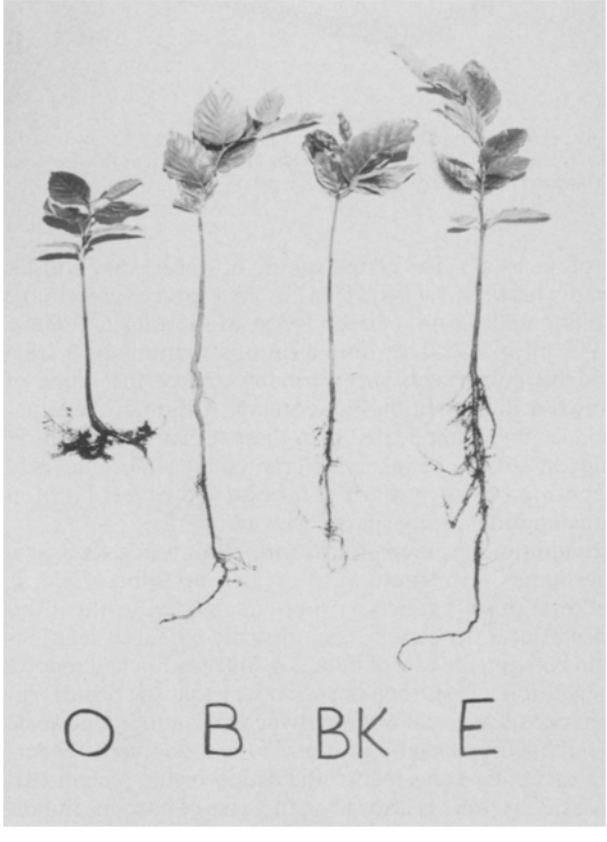

Figure 2. Different development of the root systems of beech seedlings with regard to different soil treatment after 16 months of growth. The experiment was carried out in the Haard, NRW. The different treatments were: 0, no treatment, the plants were planted in the topsoil. B, the topsoil was mixed with the mineral soil. BK, the topsoil was mixed with the mineral soil together with added lime. E, the forest soil was taken away and exchanged with nursery soil, which is used for nurseries and by gardeners.

Figure 3. Natural regeneration of beech near the stem base of a dominant tree which is under the influence of acid deposition. Egge-Gebirge, Forstamt Horn, NRW. The dieback of the beech seedlings proceeds form the base of the stem of the dominant tree.

theory that acid deposition has an impact on the physiology of trees via aluminium toxicity. A diagnosis of the action of acid deposition, apart from changes in the soil chemistry or morphology and fine anatomy of the root system has been worked out from a completely different scientific point of view. It could be shown that, depending on the prior state of the soil and the intensity of acid deposition, a whole series of events occur in the biology, microbiology and enzymology of the soils which lead to the following changes which can be detected with appropriate methods: changes in humus morphology[8], changes in the rate of N-mineralization, ammonification and nitrification, changes in the biochemical pathway of nitrification from autotrophic to heterotrophic nitrification, as can be detected by the differential activity of nitrapyrin on nitrification, changes in total soil-enzymatic activity and relative distribution over the soil profile (for details see Hüttermann[19], Hüttermann and Gehrmann[22] and Hüttermann et al.[23]).

However, arguments against the possible involvement of acid deposition can only be valid if results of experiments such as those described above are taken into account.

Mechanism of Al-toxicity: inhibition of ion uptake and replacement of Ca at the exchange sites of the cell wall matrix

If acid deposition and aluminum toxicity is to be shown to be responsible for root damage, a mechanism has to be demonstrated which can explain the following features of root dieback in the forests and aluminum effects (which presumably occur in nature, too, but have yet to be shown there) on spruce roots in hydroculture:

1) The best growth of roots occurs in the forests in those soil horizons with the highest content of humic substances (fig. 1): mixing of the mineral soil with the forest floor leads to considerable detoxification.

2) The most prominent damage which can be seen in roots from acid soils is the necrosis in the region of the endodermis, together with damage in the meristematic region of the root tip.

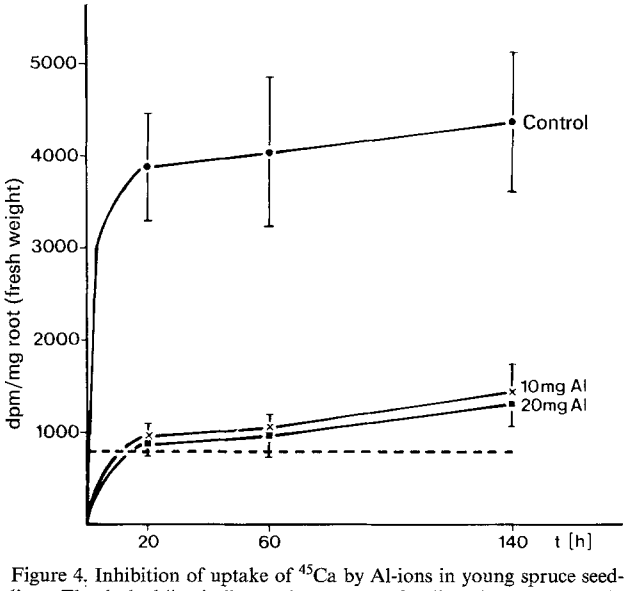

Figure 4. Inhibition of uptake of ^{45}Ca by Al-ions in young spruce seedlings. The dashed line indicates the amount of radioactive Ca present in the medium (equivalent to 4 mg of Ca/l medium).

3) Low dosages of Al^{3+} actually stimulate root biomass formation in hydrocultures, with a very pronounced induction of side root formation. The apical dominance (hormonal control) of the root tip is disturbed[41,43].

The first experiments which led to an understanding of the mechanism of action of Al on spruce roots came from Rost (quoted by Ulrich[45]), who measured the influence of Al on root length, and showed that it is not the absolute Al-concentration that is important for its action, but two factors; one is the pH (it must be below 4.2) and the other the ratio Ca/Al. At Ca/Al ratios below 1, a significant effect of Al on root lengths and side-root induction was observed, provided that the pH was below 4.2. In addition, Rost found that if Al^{3+} was masked by chelating agents like EDTA, no effect whatsoever was observed.

The second contribution to the understanding of the action of Al on the root system of spruce came from the studies of Prof. Bauch in Hamburg. He measured the ion-content of the cell walls of healthy and diseased trees of fir and spruce with the Lamma 500 mass spectrometer ion-probe[4]. The authors could show that in the cell walls of healthy plants, a rather high content of Ca and Mg was detectable, together with low concentrations of Al. In the cell walls of the roots of diseased trees, however, no Mg or Ca was found and only Al was present as the major cation[3,4].

These very elegant studies were confirmed by Junga, using a completely different method[26]. Using ^{45}Ca as tracer, he could show that at low pH values the presence of Al inhibits the uptake of Ca into both the roots (fig. 4) and the shoots of plants (fig. 5). The kinetics of the uptake

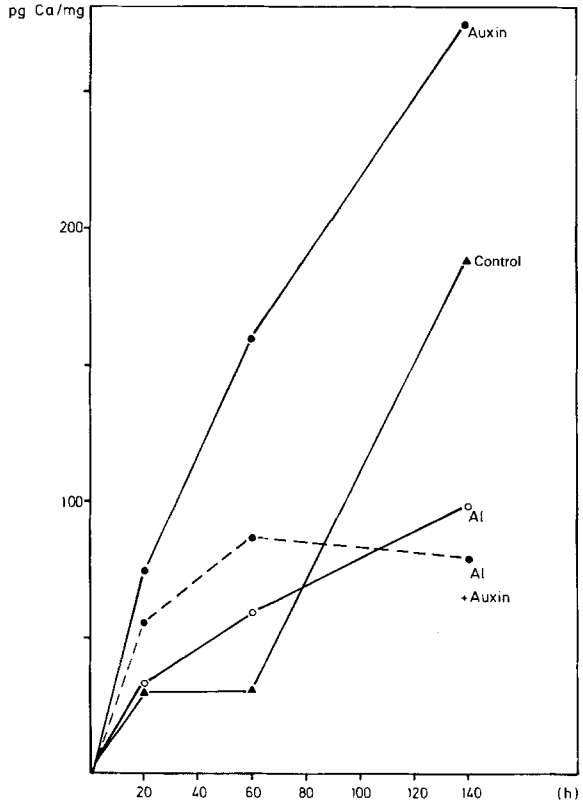

Figure 5. Inhibition of translocation of ^{45}Ca by Al-ions. The data are expressed as pg Ca/mg freshweight of sheet of the spruce seedlings.

into the roots indicate that the greater part of the Ca is taken up rather rapidly by an ion-exchange mechanism, which is completely inhibited by Al, whereas there is a much slower uptake, probably into the cells, which is not affected by this toxic ion. This interpretation could be supported by a series of experiments using certain antibiotics. Ionophore antibiotics which act directly on the cell membranes making them permeable to ions, did not affect Ca-uptake at all, whereas compounds which chelate Ca-ions, like polymyxin-B, inhibit Ca-uptake into the roots.

From these results it is apparent that at low pH-values Al acts on the roots by replacing Ca-ions in the matrix of the cell walls. This view has been confirmed in the meantime by Tischner and Stelzer (personal communication) using an electron microscope equipped with an ion probe (Ortek, EDS II).

They found indeed in spruce roots which have been subjected to Al-ions in hydroculture a build up of Al, replacing Ca in the cell walls of the root cortex, with the highest Al-concentrations in the outer walls at the beginning of the experiments. Since the rigidity of the cell walls is very much affected by this exchange of ions[13], it is obvious that the meristemic regions of the root should exhibit the highest sensitivity to Al-ions, together with the region of the endodermis, where the Al-ions eventually accumulate (Runge, personal communication).

Considering the large difference in binding constants between Al and Ca and Mg ions, with Al binding about 1000 times more strongly to pectins than Ca and Mg[27], it is not surprising that Al inhibits breakage in the region of the meristem and the endodermis-pericycle, which are exactly the places where necrosis of the cells is to be observed in acid soils[20].

This immediate action of Al on root dieback may, however, only be one of many less visible symptoms of soil acidification. One possible line of evidence may be derived from two apparently completely independent observations on lignin synthesis and lignin content in diseased trees. The study of Westermark[50] on the mechanism of lignin polymerization showed that the most probable mechanism which leads to lignin formation is phenolic coupling by the superoxide radical. This radical is stabilized by the Ca-content of the primary cell wall, which is about 50 mM in healthy tissues. These findings of Westermark are consistent with the ones of Wardrop[48], who found a level of Ca in lignified cell walls which was up to 20 times higher than in unlignified cells. The definite and high inhibition of Ca-uptake and transport by Al and acidity in acid soils[1,42] could well explain the findings of Frenzel on disturbances of lignification in diseased trees of fir and spruce on the basis of inhibition of lignification due to Ca-deficiency, rather than by lignin degradation in situ, which is the author's explanation[14].

Preliminary results on the possible involvement of other factors (e.g. photo-oxidants)

As mentioned above, it is important to consider the possible effects of other factors which may be involved in the dieback of the German forests in addition to the mechanisms outlined so far.

For an evaluation of the possible stress factors acting on a given forest ecosystem, a diagnosis program has been suggested which is based on physiological and biochemical parameters[20]. Although the studies are far from complete, some preliminary results can be given already. On the basis of the visible symptoms published by Prinz et al.[38], any massive and dominant involvement of ozone as the main factor responsible for forest decline can be excluded so far for our study area (Hamburg, Hils, Egge-Gebirge, Hilchenbach). Prinz et al.[38] showed that after the exposure of spruce trees to ozone, the needles turned completely yellow in a rather conspicuous way. Such dramatic changes in color of the needles have not been found in the more than 100 trees which have been studied so far, ranging in their needle-percentage from over 85 to 28%.

The view that photo-oxidants do not play the decisive role in the dieback in the region we studied is supported, in addition, by more detailed biochemical and physiological studies; examples are given here in the form of preliminary data for one study area, the Egge-Gebirge in Nordrhein-Westfalen.

In September 1983, six spruce trees were harvested and analysed as outlined below. The trees were taken from one plot, and selected for differences in advancement of the disease: two rather healthy trees, two with medium damage and two with heavy damage. The differences in the state of health of the trees can best be shown by the needle-percentage of the different classes (fig. 6). The data are given only for one of each pair of trees; the other had similar patterns of foliage. The six trees were analyzed for the following parameters: leaching of ions from the needles, chlorophyll content, starch content and enzymic activities of acid phosphatase and peroxidase.

Changes in the permeability of the cell membranes of the needles have been described by many authors as the result of fumigation either with SO_2[31,36] or O_3[29,38]. The model proposed by Bosch et al.[7] for the explanation of the magnesium-depletion in the needles analyzed by the authors suggests that foliar leaching derived from either ozone action and/or frost damage is one major factor responsible for forest dieback. We therefore analyzed the

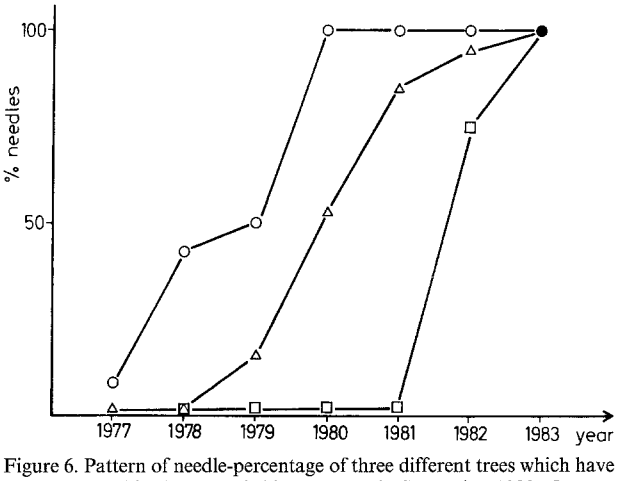

Figure 6. Pattern of needle-percentage of three different trees which have been harvested in the Egge-Gebirge, NRW, in September 1983. ○, considered to be healthy without visible damage, class 1 of damage; △, medium damage visible, class 2 of damage; □, very severe damage visible, class 3 of damage. These trees represent the classes of damage referred to in tables 1 and 2.

Table 1. Content of chlorophyll, starch, phosphatase and peroxidase in the needles of spruce trees showing different degrees of damage

Degree of damage	Tree	Chlorophyll mg/g	Starch mg/g	Phosphatase relative units	Peroxidase relative units
No visible damage	1	1.41*	7.3	0.38	0.42
		1.57; 1.41; 1.19**	8.2; 4.8; 8.6	0.64; 0.33; 0.25	0.39; 0.45; 0.13
	2	1.47	8.3	0.55	0.70
		1.41; 1.54; 1.49	8.3; 9.5; 7.7	0.35; 0.37; 0.35	0.42; 0.91; 0.73
Medium damage	1	1.33	9.4	0.75	0.63
		1.24; 1.41; 1.37	8.1; 9.9; 10.2	1.06; 0.40; 0.62	0.38; 0.82; 0.92
	2	1.66	8.5	0.98	0.72
		1.19; 1.85; 1.71	7.0; 11.1; 7.2	0.54; 0.74; 1.66	0.49; 0.67; 0.94
Heavy damage	1	1.13	8.1	0.59	0.37
		0.87; 1.14; 1.31	5.1; 9.1; 8.4	0.61; 0.61; 0.56	0.13; 0.31; 0.70
	2	1.31	7.0	1.34	0.44
		1.27; 1.35; 1.33	6.9; 8.2; 6.4	1.29; 1.47; 1.12	0.39; 0.44; 0.51

* The upper figure gives the mean values of determination of 4–6 twigs taken at different heights from the tree (10th, 20th and, if available 30th node). ** The lower figures give the mean values with regard to the age of the other needles (from left): oldest available needles from 1982, needles from 1983.

Table 2. Leaching of electrolytes from the needles of spruce trees showing different degrees of damage (30 min incubation of 5 g fresh needles in 20 ml quarz-distilled water)

Degrees of damage	Tree	Age of needles (leaching is given in $\mu s\ cm^{-1}$) 1983	n	1982	n
No visible damage	1	1.6 ± 0.4	(5)	2.6 ± 0.9	(5)
	2	1.6 ± 0.4	(6)	1.5 ± 0.8	(6)
Medium damage	1	1.4 ± 0.4	(6)	3.5 ± 1.3	(6)
	2	1.9 ± 1.0	(4)	2.0 ± 0.8	(4)
Heavy damage	1	1.5 ± 0.3	(4)	3.0 ± 0.5	(4)
	2	1.9 ± 0.7	(6)	2.9 ± 0.9	(5)

leaching of 5 g needles (fresh weight) in 20 ml quarz-distilled water, monitoring it for 30 min with a conductivity electrode. For an evaluation of the influence of differences in exposure to any damaging factor from the air, the two last annual sets of needles were analyzed separately. As is evident from table 1, no correlation can be seen between leaching and the degree of damage. In addition, the degree of leaching as a whole is much lower than would be expected from the data of Prinz et al.[38], for cation leaching after ozone-fumigation of spruce. Using their data and calibrating ion content vs conductivity, at least some 10 $\mu s\ cm^{-1}$ should be measurable if ozone were a major factor responsible for the damage of the trees.

Lichtenthaler and Buschmann[33] describe the action of photo-oxidants as being via photobleaching of photosynthesis pigments. Similar conclusions are drawn by Prinz et al.[38] and Prinz[39] which indicate, too, that ozone destroys the chlorophyll content of the needles. Destruction of the chloroplasts even to the extent that no visible functional organelle is left has been described by Fink[11] for spruce trees from the Black Forest. From the data given in table 2 for the chlorophyll contents of the three different health classes of spruce, we can exclude such a mechanism in this case. No dramatic difference in chlorophyll content was observed in the six trees in different states of health. Similar results were found for spruce trees from Hamburg[21].

Pathological accumulation of starch is a topic which has been discussed by some authors as a factor concomitant with decay diseases of spruce and fir[12,28]. Again, no indication of any pathological starch accumulation could be found in our trees (table 2), and the same results were obtained in the studies in Hamburg[21].

The activities of the two enzymes peroxidase and phosphatase react very sensitively to the presence of air contaminants like SO_2 and ozone[11,25,30,31] (to quote only some authors). We therefore measured the activities of these two enzymes, which are easy to determine, in extracts made from needles from the six different spruce trees mentioned above. The data given in table 2 again indicate no significant pattern with regard to damage, except the very damaged tree No. 2, which had extremely high values of acid phosphatase (table 2). The peroxidase-values, however, did not change with regard to the degree of damage.

Since the three classes, which were significantly different in the stage of advancement of the disease, did not show any signs of differential reaction toward the air pollutants which are being discussed at present, the only factor which seems to be left to be responsible for the damage observed is the soil. Such dramatic differences could be expected even within the same stand, because of the micro-heterogeneity of a declining ecosystem (Ulrich, personal communication).

Although the mechanisms are not yet clearly understood, and big gaps in knowledge still exist, it can already be concluded that it has not yet been possible to disprove the hypothesis of Ulrich[44] that soil acidification is the major factor causing the forest decline which is observed at present in Central Europe.

The overall picture, however, can be assumed to be much more complex, and direct action of air pollutants, especially in certain regions, may play an important role, too, especially when the soil-borne stress makes the plants much more susceptible for such airborne factors.

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