T. Schneider (Editor)/*Acidification and its Policy Implications*

STUDIES ON NORWAY SPRUCE (PICEA ABIES KARST.) IN DAMAGED FOREST STANDS AND IN CLIMATIC CHAMBERS EXPERIMENTS

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ABSTRACT

If the monitored air pollution values are compared with the air quality criteria it becomes apparent that in many parts of Europe high concentrations of ozone, extremely risky to vegetation, are formed in the summer months (May to September) with their high intensities of solar irradition. After 12 weeks of experimental exposure to 194 $\mu g\ O_3/m^3$,spruce clone needles exhibited increased intercellular areas associated with increased internal surfaces and raised internal/external surface quotients if compared to the reference trees. After exposure to 292 $\mu g\ SO_2/m^3$ over the same period, however, the intercellular system and both the other values were reduced. The histological changes of the Black Forest spruce trees corresponded to the experimentally ozone-induced ones whereas the changes of tissue of the Fichtel Gebirge samples were similar to those recognized after experimental SO_2 exposure. Both the needles of the samples exposed to either O_3 or SO_2 and the needles of the severely damaged field study items exhibited reductions of transpiration and water potential as well as reduced photosynthetic rates; simultaneously the osmotic potentials of all samples were raised due to the raised total sugar contents. Despite of comparatively lower contents of the needles, leaching experiments with Black Forest needles produced higher magnesium and calcium leaching rates than the corresponding experiments with Fichtel Gebirge needles. That the sulfur contents of the Black Forest needles were significantly lower than those of the Fichtel Gebirge items reflects the difference in SO_2 concentrations the two sites are exposed to.

INTRODUCTION

It is widely held that ozone is a major damage inducing cause of the present forest decline in the Federal Republic of Germany. However, given the air pollution conditions with long-term exposures to relatively low concentrations and with various phytotoxic components occuring simultaneously, it is rather difficult to prove the causes directly. That is why different methods have to be applied to countercheck the diagnosis. In the first part of the following paper the ozone - induced risk for vegetation will be outlined by comparing the monitored rates of air pollution with the a priori knowledge derived from dose-response studies. In the second part results of a still progressing programme on the causes of the present forest damages are reported comparing the results of experimental exposures to ozone (O_3) and sulfur dioxide (SO_2), singly and in combination, with the responses to air pollution exhibited by damaged spruce stands in the Black Forest and in the Fichtel Gebirge.

MONITORED AIR POLLUTION VALUES AND AIR QUALITY CRITERIA FOR OZONE IN COMPARISON

Based on the analysis and evaluation of the world-wide observed quantitative relations between the ozone concentrations of the air and the effects on plants the following air quality criteria were developed.

Table 1. Proposed maximum acceptable ozone concentrations for protection of vegetation (1)

Exposure Duration h	Resistance level					
	Sensitive		Intermediate		Less sensitive	
	$\mu g/m^3$	ppm	$\mu g/m^3$	ppm	$\mu g/m^3$	ppm
0.5	300	0.150	500	0.25	1.000	0.50
1.0	150	0.075	350	0.18	500	0.25
2.0	120	0.060	250	0.13	400	0.20
4.0	100	0.050	200	0.10	350	0.18

If these exposure-duration patterns are observed most plant species should be protected from acute damaging effects of ozone as single component. With long-term exposures, however, even lower concentrations of ozone may damage plants as the results from the National Crop Loss Assessment Network (NCLAN) of the United States have shown (2). Yield reductions of 10 per cent were observed in sensitive plant species at seasonal 7h/day mean ozone concentrations of only 0.028 to 0.033 ppm. Accordingly, even a mean concentration of 0.04 ppm during the growth period must be regarded as a potential danger to sensitive agricultural and horticultural plants (3); and perennial plants should be particularly affected because in the course of time subtle effects not only add up to significant growth reductions, they also reduce the resistance of the plants to other stress factors. Other phytotoxic components, such as sulfur dioxide, nitrogen dioxide and acidic precipitation occuring simultaneously are to increase this danger even more (4).

Air analyses carried out at many places, particularly in the last two decades, agree on the fact that in Europa "anthropogenic" ozone and other photo-oxidants are formed mainly during the summer months (May to September) with their high intensities of solar irradiation (5). If the monitored air pollution values are compared to the air quality criteria mentioned above it has to be recognized that the industrial conurbations, heavily affected by the precursors nitrogen dioxide and reactive hydrocarbons, exhibit the highest peak concentrations up to occasional 1/2 h-concentrations of more than 0.20 ppm. In these areas the short-term levels as shown in table 1 are frequently exceeded and acute damaging effects have consequently to be expected, whereas in rural peripheral areas, and particularly at higher altitudes in the German mountains, medium long-term concentrations were measured that very likely will cause chronic and subtle effects.

MATERIAL AND METHODS

The geobiological studies presented here were conducted at 40 to 60-years-old spruce trees in both the Fichtel Gebirge (Schneeberg, 1000 m above sea level) and the southern Black Forest (Belchen, 1050 m above sea level) in May/June, September and December 1985. At these sites the conditions of air pollution load vary remarkably: whereas the vegetation of the southern Black Forest is endangered particularly by high ozone concentrations, high SO_2-concentration characterize the conditions in the Fichtel Gebirge (6). The test trees were situated in the vicinity of monitoring stations at which continuous measurements of acidic precipitations, SO_2, O_3 and NO_x are carried out. With the experiments progressing, the biological results will be shown against the chemico-physical values of the air analyses. Both an apparently healthy or only slightly damaged spruce tree (damage class 0) and a neighbouring damaged tree - damage class 2 to 3 - were selected as test items. The test needles were sampled from the middle crown, 10 to 14 m above ground level.

In the course of the climatic chamber experiments, the equipments of which have already been described (7, 8) 3-year-old spruce clones were, singly or in combination, exposed to sulfur dioxide (292 $\mu g/m^3 \pm 15$ μg) and ozone (194 $\mu g/m^3 \pm 15$ μg) for 12 weeks. Both the climatic chamber experiments and the geobiological studies included (apparent) photosynthesis and respiration measurements using a cuvette with a O_2 electrode (Hansatech). The light energy was 300 $\mu E/m^2/sec$. The total sulfur content was determined with a Fischer-S-analyzer (model 475), with high temperature pipe stills, the Mg- and Ca-contents, both in the needles and in the leaching solutions, were AAS-measured. The spruce twigs were laid into destilled water for 4 days before carrying out the leaching measurements. The chlorophyll content was measured photometricly

(9), the Anthron method (10) was used to determine the total sugar content. To prepare for the histological analyses needle pieces, fixed in potassium bichromate - OsO_4, were embedded in styrol-methacrylate and contrasted by uranyl acetate and lead citrate. The samples were analysed by means of a transmission electron microscope Hitachi H 300. For the quantitative histological interpretation 10 sections per sample were selected.

HISTOLOGICAL AND CYTOLOGICAL ANALYSES

In the quantative approach to the histological analysis of the climatic chamber experiments, spruce needles revealed differences in the effects of sulfur dioxide and ozone. In comparison to the control items an enlarged intercellular area of the primary needles (Fig. 1A) could be recognized after O_3 exposure, associated with an enlarged internal surface and consequently a raised internal/external surface quotient (Fig. 1B). Exposures to SO_2 caused the opposite response; both the intercellular system and the internal surface were reduced, and the internal/external surface quotient had decreased. Combined exposures to O_3 and SO_2 caused no significant changes of the relative intercellular area, allowing the conclusion that opposing effects can neutralize each other. The internal/external ratio, however, was increased, corresponding to the value after O_3 exposure.

Comparing these results to those of the geobiological studies (Fig. 2), the 1- and 2-years-old needles of the damaged Black Forest spruce tree exhibit the full range of characteristical responses to O_3; both the intercellular system and the internal surface were enlarged and the internal/external surface quotient was increased. In the Fichtel Gebirge, however, the opposite results were to be recognized. With a slight decrease of the intercellular area (Fig 2A) both the internal surface and consequently the internal/external surface quotient are significantly reduced (Fig. 2B).

Ultrastructural analyses revealed a wide-ranging disintegration of the damaged Black Forest tree chloroplasts. Compared to the reference tree the grana were reduced in number and wider distributed. The granathylakoids tended to dilation. The amount of translucent plastoglobules was increased. Chloroplasts of the damaged needles have membrane bound vacuoles that develop along the chloroplasts and between the thylakoid membranes as well. In stroma the electron translucent plastoglobules increased in both number and size, compared to those in the reference series chloroplasts. The chloroplast changes in the needles of the damaged Fichtel Gebirge tree corresponded widely to the Black Forest symptoms of damage.

The damaged trees exhibit both a starch congestion and an increased tannine accumulation (Fig. 3). The vacuoles are sometimes densely filled with tannine corpuscles. Large numbers of tannine filled vesicles can be found in the cytoplasm particularly next to the vacuole. In addition, tannine corpuscles were exhibited by the needles of the damaged Fichtel Gebirge tree between the cellular wall and the plasmalemma and in the intercellular space.

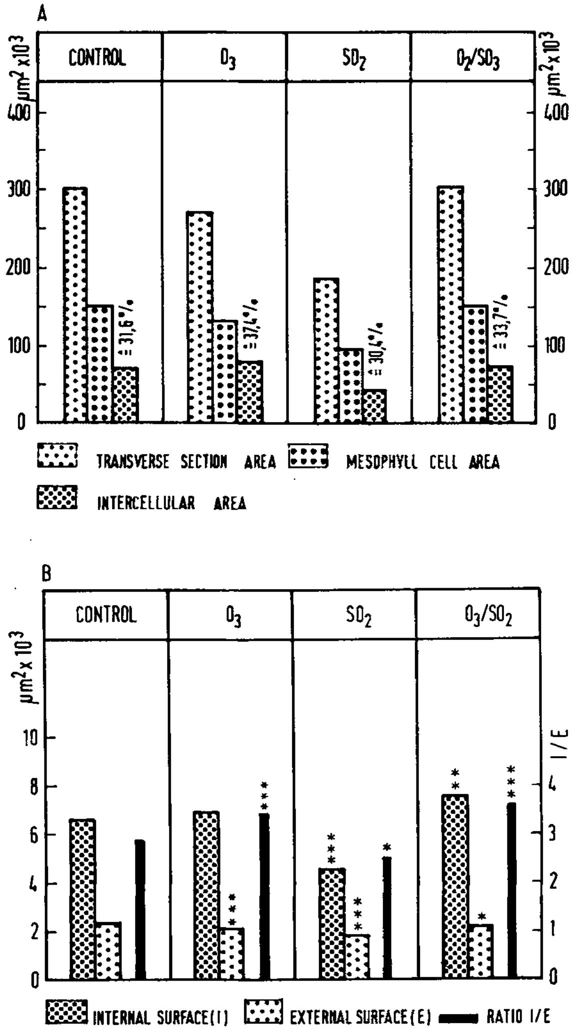

Fig. 1. Results of histological studies on 1-year-old spruce needles after exposure to O_3 and SO_2, singly and in combination

A. Effects on transverse section area, mesophyll cell area and intercellular area; the intercellular area values are given as absolute figures and as percentages of the mesophyll area

* P - 0.05 ** P - 0.01 *** P - 0.001

B. Effects on internal surface (I), external surface (E), and ratio (I/E)

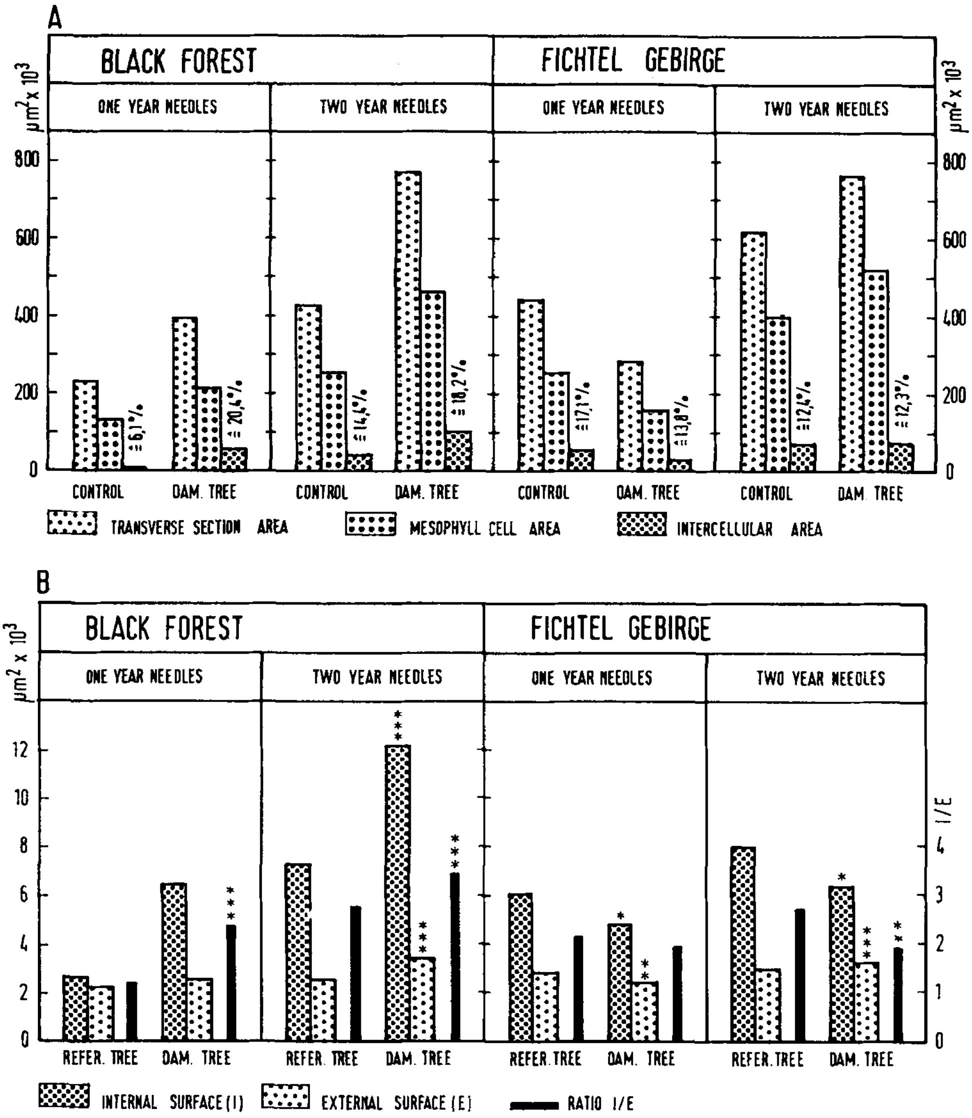

Fig 2. Results of histological studies on 1-year and 2-year old needles of Black Forest and Fichtel Gebirge spruce trees

A Effects on transverse section area, mesophyll cell area and intercellular area; the intercellular area values are given as absolute figures and as percentages of the mesophyll area

* P - 0,05 ** P - 0,01 *** P - 0.001

B Effects on internal surface (I), external surface (E), and ratio (I/E)

Fig. 3. 1-year-old spruce needle mesophyll cell of a damaged Fichtel Gebirge sample - starch congestion in the chloroplasts, disintegration of the thylakoids and tannine accumulation in the vacuole

STUDIES ON PHOTOSYNTHESIS, RESPIRATION AND TOTAL CHLOROPHYLL CONTENT

Both in the Fichtel Gebirge and in the Black Forest the only minimal damaged reference trees exhibited clearly higher apparent photosynthetic rates than the test trees with medium to severe damages (Fig. 4A). Even if the photosynthetic rates of the reference trees decreased with increasing needle ages, they remained on a high level compared to those of the damaged trees. Because the respiration rates of the reference trees decreased as well with increasing age of the needles, all needle ages exhibited positive metabolic rates.

Unlike the reference trees, the photosynthetic rates of the damaged spruce trees decreased drastically with increasing needle ages; the respiration however, was stimulated remarkably (Fig. 4B). So the provision of carbohydrates of a damaged tree in the Black Forest that possessed only 3 needle ages was

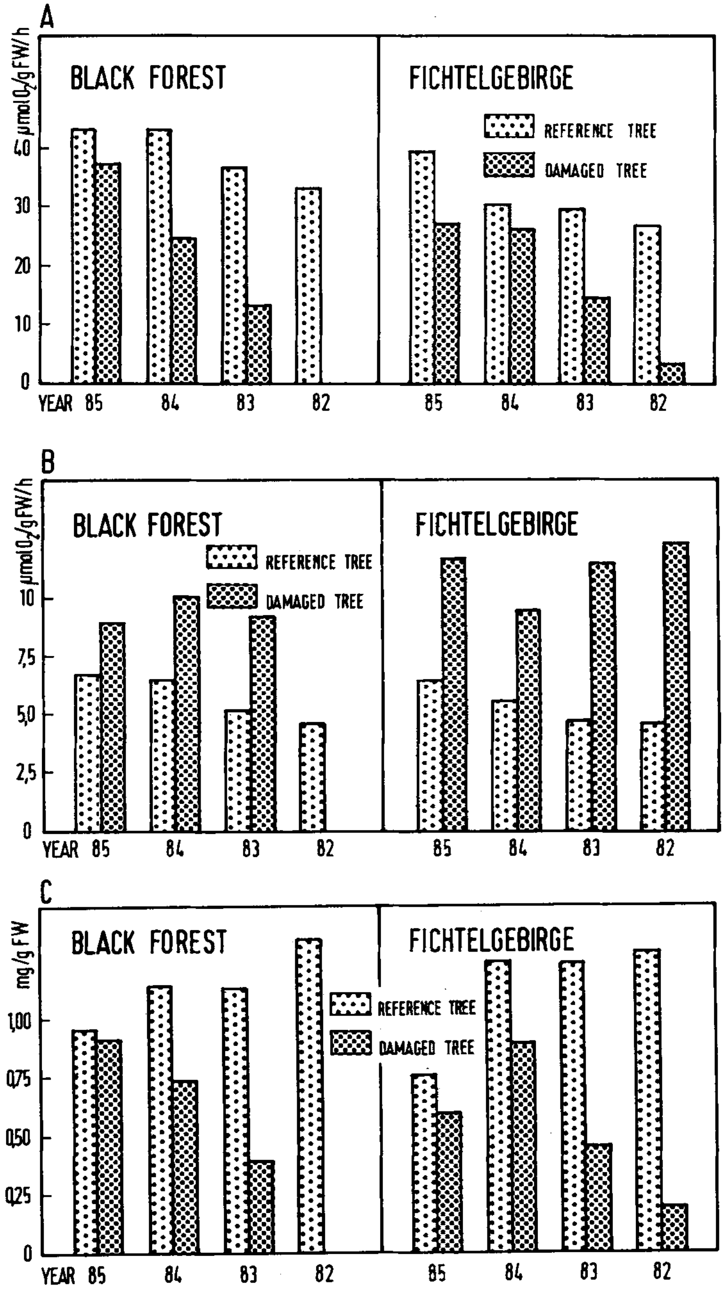

Fig. 4. Apparent photosynthesis (A), respiration (B) and total chlorophyll content (C) of the reference trees and damaged trees in the Black Forest and in the Fichtel Gebirge

confined to the positive photosynthetic rates of only two needle ages.

Exhibiting approximately the same concentrations at both sites, the total chlorophyll content of the reference trees increased markedly with the needle ages (Fig. 4C), whereas the content of the damaged trees decreased rapidly, in the 3-years-old needles to about 50%, in the 4-years-old needles of the Fichtel Gebirge samples even to a little more than one fifth of the 1-year-old needle concentration rates.

TRANSPIRATION, WATER POTENTIAL AND OSMOTIC POTENTIAL

If transpiration rates, water potential and osmotic potential, i.e. the parameters to determine the water economy, are compared with the individual photosynthetic rates after experimental O_3 and SO_2 fumigations, a close connection between the photosynthetic rate and the reduction of both transpiration and water potential is to be recognized (Fig. 5). Inversely proportional were the changes of the osmotic potentials, their increases being connected with elevated total sugar contents.

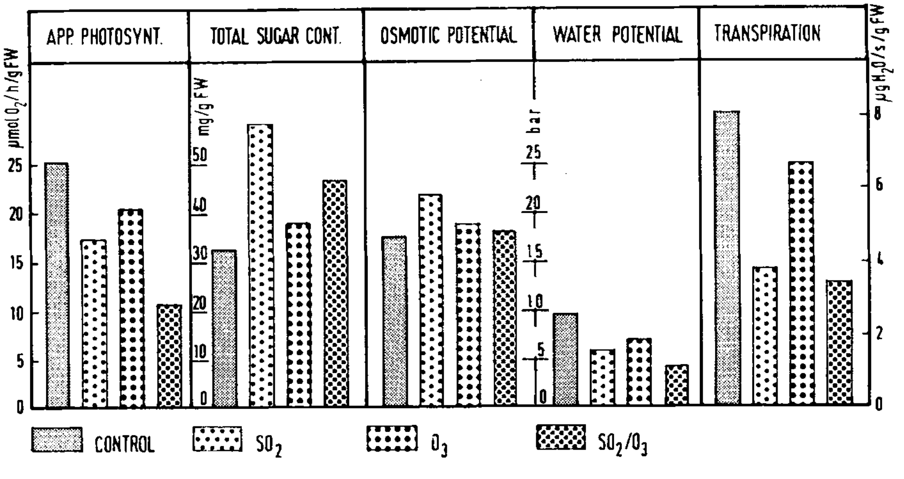

Fig. 5. Apparent photosynthesis, total sugar content and water economy of spruce clones after exposure to sulfur dioxide and ozone, singly and in combination

In general, the same results were provided by the geobiological studies (Fig. 6, 7). But because transpiration and water potential have to undergo various diurnal changes, a damaged Fichtel Gebirge spruce tree exemplifies the diurnal courses of these two criteria (Fig. 6). Even if at noon stress time the reference tree achieved remarkably higher maximum rates of both water potential and transpiration than the damaged tree. The fact that both spruce trees exhibited similar diurnal courses of the parameters, however, indicated that the damaged tree had not yet lost its capacity to regulate its water economy.

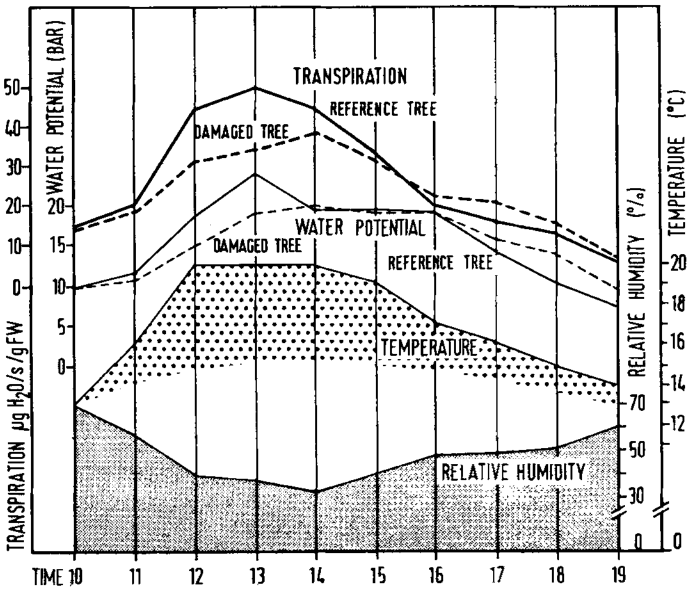

Fig. 6. Diurnal water economy rates of the reference tree and the damaged tree in the Fichtel Gebirge

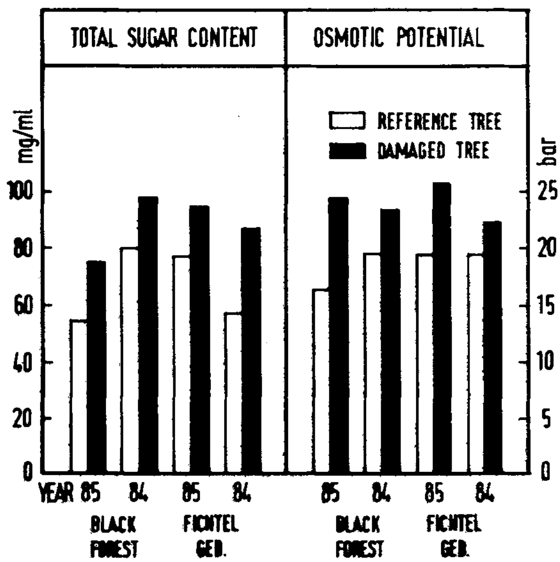

Fig. 7. Osmotic potential and total sugar content in the pressed sap of reference trees and damaged trees in the Black Forest and in the Fichtel Gebirge

As under laboratory conditions the damaged trees of the geobiological studies revealed elevated total sugar contents and raised osmotic potentials (Fig. 7); withering had very likely already begun. Despite the elevated driving potentials the damaged spruce trees were not capable to compensate the water deficiency any longer.

STUDIES ON MINERAL CONTENTS

Analyzing the calcium and magnesium concentrations of the needles of both the reference trees and the damaged trees (Tables 2 and 3), we found that:

- the Fichtel Gebirge trees showed higher mineral contents,
- the contents varied markedly in needles of different ages,
- high seasonal changes in concentrations are evident, and
- the needles of the damaged trees had lower overall concentrations.

Table 2. Contents and leaching rates of Ca in spruce needles of reference (RT) and damaged (DT) trees of the Black Forest and the Fichtel Gebirge

Year	Item	May/June		September			December	
		RT	DT	RT	DT green needles	DT yellow needles	RT	DT
		BLACK FOREST						
1985	content (mg/g DW)	1.01	1.09	2.70	3.34	1.03	1.30	0.68
	leaching (mg/g DW)	0.070	0.105	0.400	0.172	0.251	--1)	--1)
	leaching (% of content)	7.0	9.6	14.8	5.1	24.3		
1984	content (mg/g DW)	2.66	1.26	4.63	3.27	1.39	1.30	0.96
	leaching (mg/g DW)	0.017	0.012	1.305	0.189	0.157	--1)	--1)
	leaching (% of content)	0.6	0.9	28.2	5.8	11.3		
1983	content (mg/g DW)						2.65	2.43
1982	content (mg/g DW)						4.54	1.36
		FICHTEL GEBIRGE						
1985	content (mg/g DW)	2.16	1.51	4.26	3.38		3.08	1.00
	leaching (mg/g DW)	0.024	0.080	0.039	0.052		--1)	--1)
	leaching (% of content)	1.1	5.3	0.9	1.5			
1984	content (mg/g DW)	5.74	7.14	5.28	6.09		3.26	2.31
	leaching (mg/g DW)	0.005	0.009	0.030	0.045		--1)	--1)
	leaching (% of content)	0.1	0.1	0.6	0.7			
1983	content (mg/g DW)						3.18	4.22
1982	content (mg/g DW)						5.14	3.04

--1) not proved

Table 3. Contents and leaching rates of Mg in spruce needles of reference (RT) and damaged (DT) trees of the Black Forest and the Fichtel Gebirge

Year	Item	May/June RT	May/June DT	September RT	September DT green needles	September DT yellow needles	December RT	December DT
		BLACK FOREST						
1985	content (mg/g DW)	0.91	0.79	1.05	1.09	0.42	0.24	0.11
	leaching (mg/g DW)	0.235	0.042	0.014	0.161	0.039	--1)	--1)
	leaching (% of content)	25.9	5.3	1.3	14.7	9.2		
1984	content (mg/g DW)	0.31	0.22	0.77	0.93	0.35	0.13	0.10
	leaching (mg/g DW)	0.004	0.002	0.032	0.158	0.012	--1)	--1)
	leaching (% of content)	1.3	0.9	4.2	17.0	3.5		
1983	content (mg/g DW)						0.17	0.07
1982	content (mg/g DW)						0.19	0.07
		FICHTEL GEBIRGE						
1985	content (mg/g DW)	1.03	1.15	0.82	0.73		0.31	0.17
	leaching (mg/g DW)	0.119	0.161	0.007	0.017		--1)	--1)
	leaching (% of content)	11.6	14.0	0.9	2.3			
1984	content (mg/g DW)	0.73	0.82	0.78	0.81		0.28	0.33
	leaching (mg/g DW)	0.019	0.029	0.024	0.029		--1)	--1)
	leaching (% of content)	2.6	3.5	3.1	3.6			
1983	content (mg/g DW)						0.36	0.39
1982	content (mg/g DW)						0.44	0.24
--1)	not proved							

The trees of the two sites varied distincly in the supply of calcium; the calcium rates of the Fichtel Gebirge spruces were approximately twice as high as those of the Black Forest items. At both sites the calcium rates of the reference trees and of the damaged trees increased with the age of the needles. Unlike is the magnesium concentrations present a controversial picture: in the Black Forest samples they decreased markedly with increasing ages of the needles, whereas the Fichtel Gebirge items showed nothing but a slight tendency to decrease. With some exceptions, the lowest concentrations were detected in December, the decrease being more distinct in the magnesium contents. Comparing the damaged trees and the reference trees, particularly the damaged Black Forest samples exhibited lower concentrations, and again the relative difference in magnesium was greater than that of calcium.

Just as the contents of the needles, the leaching rates depend to a high degree on the site, the age of the needles and the season (Tab. 2, 3). If the full range of values of both years are compared it can be recognized that out of the

Black Forest samples higher Ca-amounts were washed than out of the Fichtel Gebirge items; both the rates relative to the needle content and the absolute rates were higher. With significantly lower Ca-contents of the needles, the concentrations washed out of the Black Forest samples were higher than those washed out of the Fichtel Gebirge items. The absolute amounts of magnesium washed out were approximately alike at both sites, the relative leaching rates of the Black Forest samples, however, were higher again. Most of the damaged trees exhibited both absolutely and relatively higher leaching rates than the reference trees, with the exception of the Black Forest reference tree and its significantly higher Ca-leaching rates. In December no calcium and magnesium concentrations could be detected in the leaching water.

Excluding the 1-year-old needles of the May/June sampling in the Black Forest, much higher total sulfur concentrations were detected in the Fichtel Gebirge samples (Fig. 8). And it was here again that the sulfur concentrations increased with the needle ages, whereas in the Black Forest such an increase could not be recognized. Over the year, the 2-years-old Fichtel Gebirge needles exhibited an increase to a December maximum. In the Black Forest the maximum rates were detected in the needles of the developing new sprouts. This rapid decrease of concentration taking place over the year is very likely due to the raised dry weight/fresh weight ratio which itself caused a diluting effect. All the other concentration rates were at about 0.9 mg/g dry substance. Unlike the Mg and Ca concentrations, the sulfur contents of the damaged trees at both sites did not differ significantly from that of the undamaged trees.

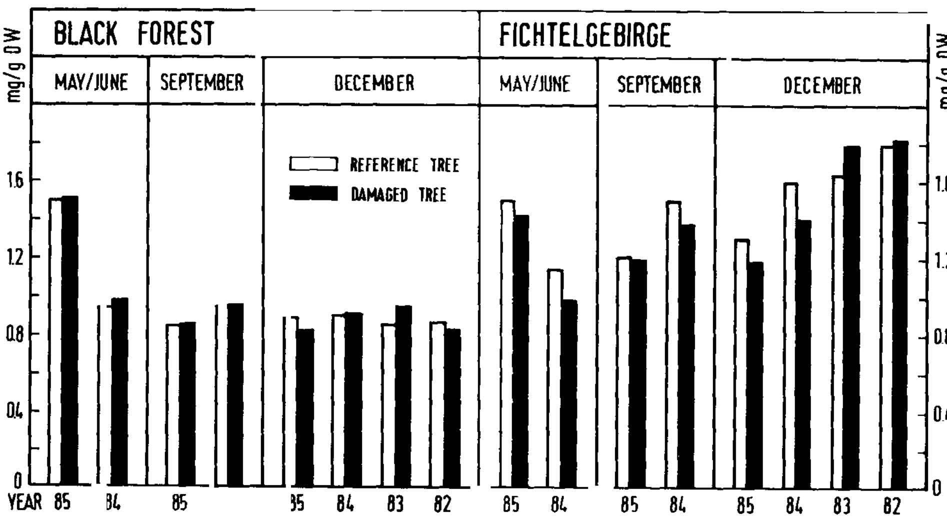

Fig. 8. Total sulfur content in the needles of reference trees and damaged trees in the Black Forest and in the Fichtel Gebirge

DISCUSSION

With the given long-term exposures to various phytotoxic air pollutants, the major components of the present forest decline can not only be determined by field studies. To countercheck the diagnosis by hypothesis testing, laboratory experiments under controlled and reproducible conditions must be added.

In both climatic chambers and small greenhouses, fumigation experiments with latent and chronic doses of ozone, sulfur dioxide and nitrogen dioxide as well as varying nutrient supplies were carried out in the course of which mottling, chloroses and necroses could be observed - injury symptoms that were exhibited by the damaged forest stands as well (4).

Some significantly similar phenomenological, physiological and histological/cytological changes in both the fumigation experiments spruce clones and the spruce trees of damaged forest stands confirm the thesis that it is mainly the combination of ozone and sulfur dioxide associated with NO_x that must be regarded as the primary and major predisposing cause of damage. The damage patterns of the Black Forest being mainly induced by ozone, that of the Fichtel Gebirge by sulfur dioxide.

Particularly after combined exposures to O_3 and SO_2, both the field studies and climatic chamber experiments needles exhibited highly hypertrophied Strasburger cells, a reduced phloem and collapses of phloem elements (8). Disintegrations of the phloem, previously observed by Fink (11) and Parameswaran (12), were associated with pathological starch accumulations in the chloroplasts and tannine accumulations in both the transfusion and mesophyll tissue. Despite reduced photosynthetic rates and increased respiration rates, raises in total sugar contents of the damaged spruce trees are observed, indicating a disturbed metabolism of the carbohydrates.

Particular attention must be given to the limited water economy. Reductions of transpiration and water potential as well as raised osmotic potential due to raised sugar contents were the responses of the climatic chamber experiments with spruce and of damaged trees in the field as well. With these disturbances of the water economies, which have been detected in the course of other studies as well (13, 14, 15), a premature senescence of the needles and restricted nutrient uptake from the soil must be expected, particularly if the nutrient supply from the soil is limited (16, 17) and the leaching of the needles is increased (18, 19).

A raised permeability of the Black Forest needle-biomembranes has to be assumed if, despite of comparatively lower contents, the Mg and Ca concentrations that have been washed out are higher than those washed out of the Fichtel Gebirge samples. Due to the significantly higher SO_2 exposures in the Fichtel Gebirge, the washout of the spruce trees "free space" should be raised if compared to the Black Forest samples.

The elevated SO_2-exposures in the Fichtel Gebirge not only caused sulfur contents of the needles that were higher than those of the Black Forest needles, but also changes of the tissue, as could be observed after experimental SO_2 exposures. Due to the higher ozone doses, the Black Forest spruce trees exhibited an enlarged intercellular system, an increased internal surface and a raised internal/external surface quotient, comparable to ozone-induced changes of the tissue as they are observed in the climatic chamber experiments.

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