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Correlations between the Mn/Ca ratio in stemflow and epiphytic lichen abundance in a dieback-affected spruce forest of the Harz Mountains, Germany

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Summary

Dieback-affected trees of a boggy stand of *Picea abies* in the Harz Mountains, northern Germany, bore a richer epiphytic lichen vegetation than healthy trees. Cover of the foliose epiphytic lichen *Hypogymnia physodes* decreased with increasing Mn/Ca ratio in stemflow. The total of lichen species per tree decreased both with the Mn/Ca ratio in stemflow and with the Mn concentration in bark. The results agree with experimental tests of Mn toxicity to *H. physodes*. Comparison with other dieback-affected spruce stands of the Harz Mountains revealed that Mn attained unusually high concentrations in the study site because of high Mn concentrations in the soil. Mn concentrations in soil, bark, stemflow, and incident precipitation suggest that *Picea abies* removes excess Mn taken up from the soil by the root system by transferring it into the bark. Mn in stemflow is supposed to derive primarily from leaching of Mn from bark and needles. SO_4^{2-} concentration that was found to be decisive for epiphytic lichen distribution in other dieback-affected spruce stands of the Harz Mountains was of subordinate significance to lichen vegetation in the present case.

Key words: bark chemistry, forest dieback, manganese, precipitation chemistry, sulphur

Introduction

Spruce stands affected by pollutant-caused forest dieback are characterized by a particularly diverse epiphytic lichen vegetation (GLIEMEROTH 1990; HAUCK & RUNGE 1999). The higher lichen diversity is correlated with lower element concentrations in stemflow and bark of affected compared to healthy trees. This difference in element concentrations is supposed to be due to needle loss of affected trees causing a reduced pollutant intercepting surface. In the Harz Mountains, HAUCK et al. (2001a) and HAUCK & RUNGE (2002) attributed the higher lichen diversity in a dieback-affected spruce stand compared to a neighboring healthy stand to lower S concentrations in stemflow and to lower concentrations of Mn and Cu in the bark of the affected stand. HESSE (2002) also discussed an influence of the S concentration in stemflow on the distribution of epiphytic lichens in a dieback-affected *Picea abies* stand.

While the cover of the foliose lichen *Hypogymnia physodes* decreased with increasing concentrations of S, Mn and Cu, respectively, cover of the crustose lichen *Lecanora conizaeoides* either remained unaffected (Mn, Cu) or followed an optimum curve (S). This different reaction agrees with the well-known fact that *L. conizaeoides* is more toxitolerant than *H. physodes* (WIRTH 1985; HAUCK et al. 2001b). Micromolar concentrations of SO_4^{2-} at pH values from 3 to 4 as found in the stemflow from the Harz Mountains have been proven to reduce the photosynthetic capacity and the rate of N_2-fixation as well as to alter the structure and the chemical composition of the cortex of lichens (LECHOWICZ 1982; HALLINGBÄCK & KELLNER 1992; PIERVITTORI et al. 1997). HILL (1971) demonstrated that *H. physodes* is much more susceptible to S than *L. conizaeoides*. Mn concentrations as found in spruce bark in the Harz Mountains are capable of inhibiting the growth of soredia of *H. physodes* (HAUCK et al. 2002a). In the soredia, the concentrations of chlorophylls *a* and *b* decrease with increasing Mn supply. Thalli of *H. physodes* absorb considerably less Mn from solution than thalli of *L. conizaeoides* (HAUCK et al. 2002b). Not yet published expe-

rimental results of our group showed that also Cu, applied in concentrations measured in spruce bark from the Harz Mountains, reduces the ability of *H. physodes* soredia to grow.

As yet, our studies of the influence of chemical site factors on lichen diversity in dieback-affected stands of the Harz Mountains have been performed at relatively high elevations at 800 m (Acker-Bruchberg ridge; HAUCK et al., 2001a; HAUCK & RUNGE 2002) and 1000 m (Mt. Brocken; HESSE 2002). In the present study, we investigated a *Picea abies* forest of the Harz Mountains at an elevation of 550 m. This study site is significantly warmer and drier than the sites on the Acker-Bruchberg and on Mt. Brocken. Yearly precipitation is 980 mm as opposed to 1500 mm on the Acker-Bruchberg and 1600 m on Mt. Brocken. Mean air temperature is 6.1 °C versus 4–5 °C and –2.8 °C (HAUCK 2000; HESSE 2002). The aim of the present study was to test the hypotheses that also at this elevation (1) epiphytic lichen vegetation is more diverse on affected trees versus healthy ones, (2) element concentrations are lower in stemflow and bark of affected trees and (3) correlations occur between the cover of lichen species and element concentrations.

Materials and methods

Studies site and selection of sample trees

The study area was a mature boggy stand of *Picea abies* (Rotes Bruch) that is situated southwest of the village Benneckenstein in the eastern Harz Mountains (52°4′ N, 10°43′ E). Affected and healthy spruce trees grew adjacent to one another within a small area. Differences in tree vitality can be attributed to differences in the ground water level. Five dieback-affected and five healthy spruce trees with a minimum diameter at breast height of 15 cm and a minimum height of 5 m were selected within a plot of approximately 50×50 m^2. The plot was non-randomly selected; search criterion was to find healthy trees and trees with damage of different severity within as small an area as possible. Trees of this area were of comparable size in height and diameter. The crown of trees classified as healthy achieved a cover of more than 75% and showed no indication of needle-yellowing. In contrast to the studies on the Acker-Bruchberg and on Mt. Brocken, where trees of different stages of defoliation were studied (HAUCK 2000; HESSE 2002), all dieback-affected trees in the present study were dead.

Mapping of epiphytic lichen vegetation

On the trunk of each sample tree at a height of 0–200 cm above the ground, cover of all epiphytic lichen species was estimated in percent (HAUCK & RUNGE 1999). When necessary species were identified by means of thin-layer chromatography (CULBERSON & AMMANN 1979). Nomenclature of lichens is based on WIRTH (1994).

Precipitation sampling and analysis

Stemflow was collected with circular gutters made of polyurethane foam. Tubes of polyvinyl chloride connected the gutters with 10 l polythene tanks (MEIWES et al. 1984). Incident precipitation was sampled in duplicate in a treeless area of the bog near the sample trees, using Büchner funnels and polythene bottles, placed 1 m above the ground, with a collecting surface each of 78.5 cm^2. Water samplers were emptied weekly during a period of 71 weeks from July 1998 to November 1999.

Samples were filtered with ash-free filters (Blue Ribbon Filters, Schleicher & Schuell, Dassel, Germany), and stored at ca. 5 °C until analysis. Each sample was analyzed separately. Electrodes were used for measuring pH (405-S7, Ingold, Wertheim, Germany) and conductivity (LF 90, Wissenschaftlich-Technische Werkstätten, Weilheim, Germany); data refer to a temperature of 25 °C. Content of K, Na, Ca, Mg, Mn, and Zn was measured with AAS (SpectrAA 30, Varian, Mulgrave Victoria, Australia). Cs^+ was used as a deionizer for K measurements, whereas K^+ was added in the case of Na and Ca, and La^{3+} in the case of Mg. Fe content was measured colorimetrically with ferrozine at $\lambda = 562$ nm (STOOKEY 1970). NH_4^+ and NO_3^- were determined by distillation using the Kjeldahl method (GERLACH 1973). PO_4^{3-} was determined colorimetrically with the molybdenum blue method at $\lambda = 700$ nm (ALLEN et al. 1974). The methylthymol blue method was applied for analyzing SO_4^{2-} content (MCSWAIN et al. 1974). This method is based on the displacement of Ba^{2+} from a methylthymol blue complex by SO_4^{2-}. The adsorption of released methylthymol blue is measured at $\lambda = 460$ nm. For each sample a blank was substracted that was analyzed with Ca^{2+} instead of Ba^{2+} in order to determine the adsorption of colored organic compounds, which interfere with the photometric measurement of methylthymol blue (CRONAN 1979).

Bark sampling and analysis

Subsequent to the last precipitation sampling, bark was collected with a knife from each sample tree. Samples were taken from a standard exposure (i.e., western exposure at a height of 100–200 cm above the ground) in order to be consistent with other studies of our group (HAUCK et al. 2001a). Epiphytes were removed from the bark surface with a wire brush before sampling. Bark samples were dried at 105 °C and homogenized in an agate mill. After acid digestion, the total content of K, Ca, Mg, Fe, Mn, Zn, Cu, and Pb was determined with AAS.

Soil conditions

Soil was sampled from twelve randomly selected sample points. It was separately collected near six dieback-affected trees and near six healthy trees in a depth of 5 and 50 cm, sieved and dried at 70 °C. Suspensions of 10 g d. wt. of soil in 20 ml of deionized water were used for determining pH (H_2O) and pH (KCl) values. After percolation with 100 mM $BaCl_2$, amounts of exchangeable K, Ca, Mg, Fe, Mn, and Al were measured with AAS. Since Mn turned out to be of special

interest as a possibly relevant site factor, the Mn concentration was additionally measured in soil extracts with 100 mM Na_2-EDTA (SCHLICHTING et al. 1995).

Statistics

Data are given as arithmetic mean ± standard error thoughout the paper. The Shapiro-Wilk test was applied for testing data for normal distribution. Significant differences between two samples were tested with Student's *t*-test for normally distributed data and with the *U*-test of Mann and Whitney otherwise. Significance of differences for more than two normally distributed samples was tested with the Scheffé test. Differences between frequency distributions were tested for significance with the chi-square test. Pearson's product-moment (r) was calculated for linear relationships of binormally distributed data, as was the non-linear correlation coefficient (r_{nl}) for non-linear relationships. When investigating relationships between element concentrations in stemflow and bark with lichen abundance, data were linearized by calculating the natural logarithm of independent and dependent parameters. Cover of the lichen *Hypogymnia physodes* was transformed according to $y' = \ln(y + 1)$, as cover values of 0% occurred. All independent variables that had statistically significant product-moment correlations after linearization, were considered in linear multiple regression analysis. For every n (total of independent variables in the model), the multiple correlation coefficient (R) was calculated for all possible combinations. The models with the highest R (for each n) are given in the results section. Statistical significance was tested by calculating F values. Spearman's rank correlation coefficient (r_s) was calculated in order to investigate the intercorrelation between element concentrations in stemflow and bark. Except for non-linear regression (Xact 4.01, SciLab GmbH, Hamburg), statistical analyses were processed with SAS 6.04 software (SAS Institute Inc., Cary, North Carolina, U.S.A.).

Results

Epiphytic lichen vegetation

Thirteen lichen species occurred on the dieback-affected trees, whereas seven species were found on the healthy trees (Table 1). The most frequent lichen species *Lecanora conizaeoides* covered more than 20% of the trunk surface on the healthy trees, but only 8% on the dieback-affected trees. *Hypocenomyce scalaris, Hypogymnia physodes* and *Parmeliopsis ambigua* grew more frequently on affected trees. *Chaenotheca brunneola, Cladonia coniocraea, C. digitata, C. polydactyla, Lepraria jackii,* and *Platismatia glauca* exhibited an insignificant trend towards higher cover values on affected trees. Three species (*Hypocenomyce caradocensis, Micarea botryoides, M. prasina*) tended to occur

Table 1. Epiphytic lichen vegetation on dieback-affected and healthy spruce trees.

	Mean cover [%]			Total of trees inhabited		
	Healthy	Affected		H	D	χ^2
Species with higher frequency on healthy trees:						
Lecanora conizaeoides	20.9 ± 3.46	7.63 ± 2.23	*	5	5	
Species with higher frequency on dieback-affected trees:						
Hypocenomyce scalaris	0.00 ± 0.00	5.03 ± 1.89	*	0	4	6.67**
Hypogymnia physodes	0.00 ± 0.00	1.25 ± 0.56	**	0	5	10.0***
Parmeliopsis ambigua	0.00 ± 0.00	0.20 ± 0.15		0	3	3.60*
Indifferent species:						
Chaenotheca brunneola	0.00 ± 0.00	0.21 ± 0.19		0	1	1.11
Cladonia coniocraea	0.00 ± 0.00	0.08 ± 0.04		0	2	2.50
Cladonia digitata	0.06 ± 0.03	0.58 ± 0.30		3	3	0.00
Cladonia polydactyla	0.09 ± 0.06	0.34 ± 0.29		3	3	0.00
Hypocenomyce caradocensis	0.16 ± 0.10	0.14 ± 0.10		2	2	0.00
Lepraria jackii	0.03 ± 0.01	0.16 ± 0.13		2	2	0.00
Micarea botryoides	0.25 ± 0.22	0.00 ± 0.00		1	0	1.11
Micarea prasina	0.80 ± 0.66	0.00 ± 0.00		2	0	2.50
Platismatia glauca	0.00 ± 0.00	0.05 ± 0.03		0	2	2.50

Notes: Cover, arithmetic mean ± standard error; calculated from mean values of eight relevés per tree; statistics: *U*-test. Frequency (on five healthy and five dieback-affected trees): Chi-square test. H – healthy trees; D – dieback-affected trees. Levels of significance: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Table 2. Amounts and element content of stemflow and incident precipitation.

	Stemflow			Incident precipitation
	Healthy	Affected		
NH_4^+ [µmol l^{-1}]	248 ± 50	46.8 ± 3.7	**	37.7 ± 5.6
NO_3^- [µmol l^{-1}]	92.3 ± 13.8	36.8 ± 5.1	*	46.4 ± 7.2
PO_4^{3-} [µmol l^{-1}]	3.76 ± 0.64	4.80 ± 1.68		0.45 ± 0.20
SO_4^{2-} [µmol l^{-1}]	75.7 ± 11.8	34.8 ± 2.9	**	17.8 ± 2.3
K [µmol l^{-1}]	245 ± 47	144 ± 44		15.4 ± 5.0
Na [µmol l^{-1}]	144 ± 10	120 ± 3.0		105 ± 18
Ca [µmol l^{-1}]	95.3 ± 23.6	92.9 ± 12.3		12.6 ± 1.6
Mg [µmol l^{-1}]	30.0 ± 3.8	27.2 ± 7.4		6.35 ± 0.57
Fe [µmol l^{-1}]	1.04 ± 0.25	0.30 ± 0.06	*	0.01 ± 0.01
Mn [µmol l^{-1}]	5.86 ± 0.76	5.33 ± 1.50		0.13 ± 0.02
Mn/Ca	0.08 ± 0.01	0.06 ± 0.00		0.02 ± 0.00
Mn/Mg	0.21 ± 0.02	0.19 ± 0.03		0.03 ± 0.00
Zn [µmol l^{-1}]	1.28 ± 0.21	1.42 ± 0.20		0.26 ± 0.03
pH	3.86 ± 0.05	3.82 ± 0.10		4.09 ± 0.05
Conductivity [µS cm^{-1}]	127 ± 22	82.0 ± 2.7		28.2 ± 2.23
Stemflow [ml $tree^{-1}$ $week^{-1}$]	1.3 ± 0.2	1.1 ± 0.2		
Precipitation [l m^{-2} $week^{-1}$]				31.3 ± 5.0

Notes: Arithmetic mean ± standard error. Levels of significance: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$ (*t*-test for difference between healthy and affected trees). Measuring period: July 1998 – December 1999 (71 weeks). Data are calculated from means of 2 × 5 sample trees over the entire measuring period (stemflow) or from weekly means of two replicates (incident precipitation).

with higher cover values on healthy trees. The total cover of all epiphytic lichens and bryophytes amounted to 16 ± 3% on the dieback-affected trees and to 23 ± 4% on the healthy ones.

Element concentrations in stemflow, incident precipitation, bark, and soil

Element concentrations in stemflow were generally higher than in incident precipitation. NH_4^+, NO_3^-, SO_4^{2-} and Fe occurred in significantly lower concentrations in the stemflow of dieback-affected compared to healthy trees (Table 2). With the other element concentrations in stemflow and with element concentrations in bark (Table 3) no significant difference was found. Element concentrations in the soil did not differ between the surroundings of healthy and dieback-affected trees; an exception was Pb with higher concentrations in the upper soil near healthy trees (Table 4).

Table 3. Element content of bark (in mmol kg^{-1} d. wt.) on dieback-affected and healthy spruce trees.

	Healthy	Affected
K	13.3 ± 3.9	11.3 ± 1.7
Ca	148 ± 11	126 ± 20
Mg	5.22 ± 0.80	5.40 ± 1.50
Fe	5.06 ± 0.60	4.86 ± 0.96
Mn	5.43 ± 1.53	2.85 ± 0.54
Mn/Ca	0.04 ± 0.01	0.03 ± 0.01
Mn/Mg	1.07 ± 0.24	0.60 ± 0.11
Zn	0.82 ± 0.16	0.76 ± 0.11
Pb	0.04 ± 0.01	0.05 ± 0.02
Cu	0.12 ± 0.00	0.10 ± 0.01

Notes: Arithmetic mean ± standard error. No significant differences (*t*-test, $P > 0.05$, $df = 4$).

Correlation between chemical site factors and epiphytic lichen vegetation

Curvilinear relationships were found between cover of *Hypogymnia physodes* and some element concentrations in stemflow (Table 5); thus, data were logarithmized for linearization to prepare them for linear multiple regression analysis. Cover of *H. physodes* decreased with increasing concentrations of SO_4^{2-}, K, and Mn in stemflow. The closest correlation was found with the molar ratio of Mn to Ca. When the effects of these chemical parameters on cover of *H. physodes* were examined in multiple regression analysis the most significant model of two independent variables was found with the Mn/Ca ratio and the K concentration in stemflow ($R = 0.94$, $P \leq 0.001$). A model of the Mn/Ca ratio and

Table 4. Element concentrations (in mmol kg^{-1} d. wt.) of soil near dieback-affected and healthy spruce trees.

	Extractant	Depth	Healthy	Affected	
K	BaCl2	5 cm	1.33 ± 0.23	1.13 ± 0.05	
		50 cm	1.13 ± 0.15	1.54 ± 0.18	
Ca	$BaCl_2$	5 cm	11.6 ± 3.2	15.4 ± 2.2	
		50 cm	8.03 ± 3.52	8.98 ± 1.88	
Mg	$BaCl_2$	5 cm	10.0 ± 3.4	14.0 ± 2.7	
		50 cm	10.1 ± 4.2	15.3 ± 3.9	
Fe	$BaCl_2$	5 cm	1.69 ± 0.44	2.20 ± 0.14	
		50 cm	0.50 ± 0.11	0.84 ± 0.13	
Mn	$BaCl_2$	5 cm	0.30 ± 0.11	0.38 ± 0.07	
		50 cm	0.27 ± 0.12	0.69 ± 0.22	
Mn	EDTA	5 cm	1.68 ± 0.73	2.50 ± 0.48	
		50 cm	1.82 ± 0.77	1.50 ± 0.31	
Al	$BaCl_2$	5 cm	5.99 ± 0.33	6.51 ± 0.11	
		50 cm	6.16 ± 0.81	10.9 ± 2.5	
Zn	$BaCl_2$	5 cm	0.88 ± 0.56	0.37 ± 0.05	
		50 cm	0.16 ± 0.07	0.08 ± 0.00	
Pb	$BaCl_2$	5 cm	0.44 ± 0.04	0.14 ± 0.02	**
		50 cm	0.04 ± 0.01	0.02 ± 0.00	
pH	H_2O	5 cm	4.31 ± 0.11	4.26 ± 0.02	
		50 cm	4.96 ± 0.22	4.93 ± 0.08	
pH	KCl	5 cm	2.95 ± 0.39	3.54 ± 0.09	
		50 cm	3.74 ± 0.24	3.88 ± 0.12	

Notes: Arithmetic mean ± standard error. Levels of significance: ** $P \leq 0.01$ (*t*-test, $df = 5$).

Table 5. Correlations between cover of *Hypogymnia physodes* and element concentrations in stemflow

	Linearized data	Original data	Regression
	r	r_{nl}	
SO_4^{2-}	−0.64*	-0.69*	$y = a + bx^c$
K	−0.79**	−0.82**	$y = a/(x + b)$
Mn	−0.75*	−0.68*	$y = a/(x + b)$
Mn/Ca	−0.82**	−0.79**	$y = a/(x + b)$

Notes: Independent parameters linearized by calculating the natural logarithm, cover of *H. physodes* linearized according to $y' = \ln(y + 1)$. Correlation coefficients are Pearson's product-moments for linearized data and non-linear correlation coefficients for the original data.

SO_4^{2-} concentration yielded a slightly lower correlation coefficient ($R = 0.93$, $P \leq 0.001$). The multiple correlation coefficient for a model of the three independent variables Mn/Ca ratio, SO_4^{2-} and K concentration amounted to $R = 0.96$ ($P \leq 0.01$). Cover of *H. physodes* also decreased with increasing concentrations of K and Mn in bark as well as with the Mn/Ca ratio in bark. However, these parameters had no significant effect in multiple regression analysis.

The total of lichen species per sample tree also decreased with increasing element concentrations

Table 6. Correlations between the total of lichen species per tree and element concentrations in stemflow and bark.

	Linearized data	Original data	Regression
	r	r_{nl}	
Mn/Ca (Stemflow)	−0.83**	−0.94***	$y = a + bx^c$
Mn/Mg (Stemflow)	−0.71*	−0.93***	$y = a + bx^c$
Mn (Bark)	−0.85**	−0.87**	$y = a/(x + b)$
Mn/Ca (Bark)	−0.77**	−0.80	$y = a/bx$
Pb (Bark)	−0.70*	ns.	

Notes: Independent and dependent variables linearized by calculating the natural logarithm. Correlation coefficients are Pearson's product-moments for linearized data and non-linear correlation coefficients for the original data.

(Table 6). Using ln-transformed data, significant correlations were found with the molar ratio of Mn/Ca and of Mn/Mg in stemflow as well as with the concentrations of Mn and Pb in bark and with the Mn/Ca ratio in bark. The closest correlations using ln-transformed data were found with the Mn concentration in bark and with the Mn/Ca ratio in stemflow. In multiple regression analysis, a model of these two parameters explained about 90% of the variation of the total of lichen species per tree ($R = 0.94$, $P \leq 0.001$). Cover of the crustose lichen *Lecanora conizaeoides* was not correlated with element concentrations in stemflow and bark, except for a linear increase of cover with increasing NO_3^- concentration of stemflow ($r = 0.78$, $P \leq 0.01$) for non-logarithmized data.

Discussion

As in the dieback-affected spruce forests at 800 m (Acker-Bruchberg) and 1000 m (Mt. Brocken) studied by Hauck & Runge (2002) and Hesse (2002), more lichen species were found on dieback-affected trees compared to healthy ones. *Hypogymnia physodes* and *Lecanora conizaeoides*, the two lichen species most extensively studied by our group have a similar distribution at all study sites. The foliose lichen *H. physodes* occurs more frequently on affected trees, whereas the crustose lichen *L. conizaeoides* is more frequent on healthy trees. Moreover, the trend for higher frequency of *Hypocenomyce caradocensis*, *Micarea botryoides*, and *M. prasina* on healthy trees is in line with the previous studies from the Harz Mountains. In contrast to the vast majority of lichen species, these species as well as *Lecanora conizaeoides* are apparently not favored by the site conditions in dieback-affected stands. Considerably less lichen species ($n = 13$) were recorded from the

sample trees of the present study at 550 m compared to the stands at 800 m ($n = 29$; HAUCK & RUNGE 2002) and at 1000 m ($n = 21$; HESSE 2002). A lower mean total of lichen species per sample of 4.9 ± 0.8 (10 sample trees) than in the stands at 800 m (9.2 ± 2.7; 81 trees) and at 1000 m (8.1 ± 0.4; 20 trees) proves that the lower species diversity at 550 m is not due to the smaller sample size, but probably due to lower elevation. Lower humidity including less fog events are supposed to be the main cause of the lower lichen diversity at 550 m. VONARBURG (1993) compared three sites with *Parmelina tiliacea* at 550, 1000 and 1600 m in Switzerland and found decreasing air and thallus temperatures as well as increasing relative humidity and increasing thallus water contents with increasing elevation.

The significantly lower concentrations of NH_4^+, NO_3^-, SO_4^{2-}, and Fe as well as similar insignificant trends of other elements in the stemflow can be attributed to decreased atmospheric interception caused by the decreased canopy surface of dieback-affected trees (HAUCK & RUNGE 2002). In accordance with our former studies, cover of *Hypogymnia physodes* decreased with increasing SO_4^{2-} concentration in stemflow. However, correlations with other parameters were considerably closer; the closest correlation was found with the molar Mn/Ca ratio in stemflow (Table 5). This parameter or the Mn concentrations in stemflow and bark were not intercorrelated with SO_4^{2-} concentration in stemflow (HESSE 2002). An interaction of Ca with Mn has already been shown for the growth of soredia of *H. physodes* (HAUCK et al. 2002 a). The inhibiting effect of Mn on the growth of the soredia was alleviated by Ca in soredia cultured on agar medium. Intracellular uptake and extracellular absorption of Mn from solution in thalli of *H. physodes* was significantly reduced when Mn was applied in combination with Ca (HAUCK et al. 2002 b). *H. physodes* soredia lost Ca from cell walls and cell lumina of the mycobiont, but not of the *Trebouxia* photobiont in cultures kept with excess Mn (HAUCK et al. 2002 a). Adult thalli were found to release significant amounts of extracellular Ca when incubated in Mn solutions (HAUCK et al. 2002 b). These experimental findings indicate that site conditions become less favorable for *H. physodes* with increasing Mn/Ca ratio. Closer correlation of the Mn/Ca ratio than of the absolute Mn concentration in stemflow with cover of *H. physodes* suggests that the former is more relevant.

The significant correlations between the total of lichen species per sample tree with the Mn/Ca and Mn/Mg ratio in stemflow as well as with the Mn concentration in bark and with the Mn/Ca ratio in bark (Table 6) suggest that high Mn concentrations are a limiting factor not only for *H. physodes*, but for most lichen species in the investigated spruce stand. Ultimately, high soil Mn concentrations might be the cause for this relationship. Absolute Mn concentrations as well as Mn/Ca and Mn/Mg ratios are considerably higher than in the soils on the Acker-Bruchberg ridge and on Mt. Brocken (Table 7). Mn concentrations as well as Mn/Ca and Mn/Mg ratios in bark and stemflow vary in accordance with concentrations and ratios of the soils. This suggests that root uptake and subsequent xylem transport determine the Mn concentration in bark and, due to leaching from bark and needles, also in stemflow. In *Populus*, SLOOF & WOLTERBEEK (1993) concluded from a concentration gradient from the youngest xylem to the bark that Mn was deposited in the bark. In cross-sections of *Picea abies*, LÖVESTAM et al. (1990) found high Mn and Ca concentrations in the bark, but low concentrations in the wood underneath. This may indicate the possible deposition of excess amounts of these elements in the bark. Ca is known to be deposited in oxalate crystals in *Picea abies* bark (SCHMIDT-VOGT 1986).

Root uptake and xylem transport of Mn can be supposed to decrease with increasing needle loss. This is in line with the (insignificant) trend for higher Mn concentrations in the bark of healthy versus dieback-affected trees. Mn concentration in bark of healthy trees ranged from 2.4 to 9.7 mmol kg^{-1} d. wt., whereas it varied between 1.3 and 4.5 mmol kg^{-1} d. wt. in bark of dieback-affected trees. On the Acker-Bruchberg ridge and Mt. Brocken, maximum concentrations in bark amounted to 2.0 and 2.4 mmol kg^{-1} d. wt., respectively (HAUCK & RUNGE 2002; HESSE 2002). Using a large sample size of 120 spruce trees sampled on the Acker-Bruchberg ridge, Mn concentrations in the bark of dieback-affected trees were found to be significantly lower than in the bark of healthy trees (HAUCK et al. 2001 a). Differences in atmospheric deposition of Mn can be ruled out as the cause for the higher Mn concentrations in bark, stemflow and soil in the present case, as Mn concentration in incident precipitation did not differ from the stands on the Acker-Bruchberg ridge and on Mt. Brocken (Table 7).

The negative correlation between *H. physodes* cover and K concentration in stemflow is probably coincidental, since not yet published experiments of our group showed that K is not taken up by *H. physodes* at concentration ranges and pH conditions that usually occur in the stemflow of *Picea abies* in the Harz Mountains. The lack of correlations between cover of the crustose lichen *Lecanora conizaeoides* and most element concentrations in stemflow or bark is in line with the known toxitolerance of the species (WIRTH 1985). On the Acker-Bruchberg ridge and Mt. Brocken, cover of *L. conizaeoides* was not affected by the Mn concentration in bark or stemflow either (HAUCK et al. 2001 a; HAUCK & RUNGE 2002; HESSE 2002). At low concentrations, *L. conizaeoides* is even favored by inorganic S

Table 7. Mn concentrations as well as molar Mn/Ca and Mn/Mg ratios in upper soil, bark, stemflow, and incident precipitation of three dieback-affected *Picea abies* stands in the Harz Mountains.

		Acker-Bruchberg		Mt. Brocken		Present study	
Soil	Mn [mmol kg^{-1} d. wt.]	0.41 ± 0.20	a	0.33 ± 0.19	a	2.09 ± 0.52	b
	Mn/Ca × 10^3	13.2 ± 1.3	a	27.3 ± 7.6	a	224 ± 109	a
	Mn/Mg × 10^3	59.4 ± 7.7	a	108 ± 29	b	364 ± 229	b
Bark	Mn [mmol kg^{-1} d. wt.]	1.27 ± 0.08	a	1.55 ± 0.09	a	4.14 ± 0.88	b
	Mn/Ca × 10^3	10.6 ± 0.9	a	9.41 ± 0.62	a	69.5 ± 6.9	b
	Mn/Mg × 10^3	268 ± 31	a	259 ± 19	a	834 ± 148	b
Stemflow	Mn [µmol l^{-1}]	3.83 ± 0.44	a	2.64 ± 0.38	b	5.60 ± 0.80	ab
	Mn/Ca × 10^3	33.0 ± 2.8	a	39.8 ± 2.2	a	69.5 ± 6.9	b
	Mn/Mg × 10^3	139 ± 13	a	108 ± 6	a	200 ± 17	b
Incident	Mn [µmol l-1]	0.17 ± 0.05	a	0.13 ± 0.02	a	0.13 ± 0.02	a
precipitation	Mn/Ca × 10^3	9.00 ± 0.65	a	18.3 ± 3.3	b	15.7 ± 2.9	b
	Mn/Mg × 10^3	81.9 ± 6.0	a	27.4 ± 4.7	b	25.4 ± 4.4	b

Notes: Data for Acker-Bruchberg from HAUCK (2000) and HAUCK & RUNGE (2002), for Mt. Brocken from HESSE (2002). Concentrations (arithemetic mean ± standard error) in soil refer to the upper soil in a depth of about 5 cm and are measured in twelve replicate samples per stand in extracts with 100 mM EDTA in the case of Mn and with 100 mM $BaCl_2$ in the case of Ca and Mg. Concentrations in bark and precipitation are total concentrations measured on 11, 20, 10 sample trees and two replicate samplers per site for incident precipitation, respectively. Precipitation measurements were carried out from April 1997 to December 1998 (86 weeks; Acker-Bruchberg), from June 1998 to November 1999 (76 weeks; Mt. Brocken) and from July 1998 to November 1999 (71 weeks; present study). It should be noted that element concentrations in stemflow and incident precipitation depend on the sampling period and that therefore values from the different sites are not fully comparable. Sample trees in each plot comprise a range of healthy to increasingly defoliated spruce trees. The values referring to the present studies are means of all ten sample trees or of all soil samples, respectively. Within a row, means sharing a common letter do not differ significantly (Scheffé test, $P \leq 0.05$).

(BATES et al. 1996; HAUCK et al. 2001 b). We have no information whether the positive correlation with NO_3^- concentration in stemflow was causal. In other spruce stands of the Harz Mountains, such correlations were not observed (HAUCK & RUNGE 2002; HESSE 2002). Aside from element concentrations in precipitation and in bark, element transfer by dry deposition or deposition with fog could affect lichen distribution in the study site; data of these parts of deposition are not available.

MACHER & STEUBING (1984) emphasized the significance of light for the higher epiphytic lichen diversity on dieback-affected *Picea abies* in the Bavarian Forest, southern Germany. For the more frequent occurrence of *Hypocenomyce scalaris, Hypogymnia physodes* and *Parmeliopsis ambigua* on the dieback-affected trees, the higher light influx on defoliated trees has to be considered as possibly relevant, because all these species tend to occur more frequently in light-flooded habitats (WIRTH 1995; BRODO et al. 2001). *Lecanora conizaeoides,* however, is indifferent to light (WIRTH 1995). In the Harz Mountains, this species colonizes shady spruce plantations as well as sun-exposed sites. Thus, its decline on the dieback-affected trees cannot be attributed to light. Unpublished light measurements of our group from Mt. Brocken confirmed the assumption that light irradiance at the tree trunks (at 1.5 m above the ground) constantly increases with increasing needle loss. However, no significant correlations with the cover of *Hypocenomyce scalaris, Hypogymnia physodes, Lecanora conizaeoides* and *Parmeliopsis ambigua* or any other lichen species were found, whereas HESSE (2002) found significant correlations with the S concentration in stemflow. Hence, it is probable that light was not decisive for the difference in the epiphytic lichen abundance in the present case either. HAUCK et al. (2000) demonstrated that water-holding capacity of *P. abies* bark was not correlated with the cover of any lichen species in a dieback-affected spruce forest in the western Harz Mountains. An unpublished study of our group in a dieback-affected *Picea rubens-Abies balsamea* forest of upstate New York, U.S.A., revealed that neither light, nor evaporation, relative humidity, air temperature or the water-holding capacity of the substrate were decisive for the higher epiphytic lichen diversity on damaged versus healthy trees. These findings indicate that microclimate in general is apparently of subordinate importance to within-stand distribution of many epiphytic lichen species in dieback affected coniferous forests.

Competition has probably not been involved in the change of the epiphytic vegetation on declining spruce trees in the sample plot. This is because less then a quarter of the available bark area was covered by lichens or bryophytes. The low epiphyte cover may be caused by

unfavorable moisture conditions and perhaps also by the high Mn concentrations in the bark and in stemflow. The low cover suggests that the toxitolerant *L. conizaeoides* did probably not decline on the dying trees, because it was overgrown by more pollution-sensitive lichens, but because the growth conditions became less favorable. WIRTH (1993) and KIRSCHBAUM & HANEWALD (2001) established a significant decrease of *L. conizaeoides* concomitant to decreasing pollutant deposition on permanent plots in Germany within five or two years, respectively, while the formerly covered bark areas were mostly not yet colonized by other epiphytes. In a coniferous forest of Great Britain that was experimentally fumigated with SO_2, cover of *L. conizaeoides* increased with increasing SO_2 concentration despite of low competition through other epiphytes in any plot (BATES et al. 1996).

Conclusions

In accordance with studies at higher elevations of the Harz Mountains (HAUCK & RUNGE 2002; HESSE 2002), epiphytic lichen vegetation was more diverse on dieback-affected trees compared to healthy ones. However, the total of lichen species was lower in this montane to submontane stand than in comparable stands of the high-montane belt. The Mn/Ca ratio in stemflow and the Mn concentration in bark are probably most significant for determining lichen distribution in the study site. This is different from the findings from other dieback-affected areas in the Harz Mountains, where S concentrations in stemflow had the closest correlations with the occurrence and the cover of epiphytic lichen species (HAUCK & RUNGE 2002; HESSE 2002). The significance of Mn can be attributed to higher Mn concentrations in the soil; Mn is supposed to be taken up by the root system of the spruce trees and transferred into the bark via the xylem. The probable influence of the Mn/Ca ratio in stemflow agrees with the alleviating effect of Ca on Mn uptake and toxicity in *Hypogymnia physodes* that was found in experiments by HAUCK et al. (2002a, b).

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