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# Relevance of element content of bark for the distribution of epiphytic lichens in a montane spruce forest affected by forest dieback

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**"Capsule":** *Bark chemistry differences affected diversity of epiphytic lichens in dieback-affected and non-affected stands of Norway spruce.*

## Abstract

Element content in the bark of Norway spruce (*Picea abies*) was measured in a montane forest heavily affected by forest dieback and compared to that in a nearby intact stand. Bark contained less S, K, Fe, Mn, Pb, Cu, and $H^+$ and more N, Ca, Mg, and Zn in the dieback-affected stand than in the intact one. Diversity of epiphytic lichen vegetation was higher in the dieback-affected stand than in the intact one. Cover of the foliose lichen *Hypogymnia physodes* was negatively correlated with Mn and Cu content of bark. Cover of the extremely acidophytic species *Lecanora conizaeoides* decreased with increasing Mg and increased with increasing Cu content of bark. The measurements support the hypothesis that chemical site factors are decisive for the high lichen diversity in dieback-affected montane spruce forests. © 2001 Elsevier Science Ltd. All rights reserved.

*Keywords:* Epiphytic lichens; Bark chemistry; Copper; Manganese; Forest dieback

## 1. Introduction

An increase in the diversity of epiphytic lichens, especially in those species known to be pollution sensitive (John, 1986; Gliemeroth, 1990), has been observed in dieback-affected montane coniferous forests of Europe. Since epiphytic lichens are known to be sensitive to acidic precipitation, especially to $SO_2$ and its derivatives (Sigal and Johnston, 1986; Nash and Wirth, 1988; Piervittori et al., 1996), this phenomenon seems to run counter to the general assumption that the decline of montane forests is caused by acid deposition. Therefore, some authors took this as an argument against this assumption (e.g. Müller, 1983; Gliemeroth, 1990; Ellenberg, 1996). Others attributed the higher lichen diversity in dieback-affected forests to increased light availability (Macher and Steubing, 1984; John, 1986). This explanation assumes that either the lichen species are suboptimally supplied with light in the healthy forests or that a higher biomass production due to an increased light supply can compensate for pollution effects.

Hauck and Runge (1999) hypothesized that epiphytic lichens are exposed to lower doses of pollutants in dieback-affected coniferous forests than in intact ones, even under similar atmospheric pollution conditions. The authors argued for the significance of stem flow as a direct source of pollutants for trunk-inhabiting epiphytic lichens. Element content of stem flow does not result solely from wet but also from dry deposition (i.e. interception of gaseous and particulate pollutants as well as of dissolved pollutants from clouds or fog). Concentrations as well as doses of pollutants could be lower in the stem flow of declining stands than in that of intact ones for two reasons: first, the lower needle mass of damaged trees results in smaller intercepting surfaces, and second, in the more open damaged stands, trunks are partly in a direct contact with incident precipitation. Measurements on the element content of stem flow in a dieback-affected spruce stand and in an intact one in the

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German Harz Mountains supported this hypothesis (Hauck and Runge, 1999).

Dissolved pollutants can affect lichens directly when thalli are soaked by stem flow. In addition, indirect effects through effects of stem flow on the chemical composition of the lichen-bearing bark are conceivable. Therefore, we tested the hypothesis that the bark of spruce trees in an intact stand and that in a dieback-affected stand differs in element content. For this purpose, those stands were compared in which differences in the chemical composition of stem flow had been established, in spite of similar element content of incident precipitation (Hauck, 1999; Hauck and Runge, 1999). In the following we will present results and discuss the following questions:

1. whether differences in element content of bark can be traced back to differences in stem flow; and
2. whether such differences are in accordance with the initial hypothesis that chemical conditions for the presence of epiphytic lichens are more favorable in dieback-affected spruce stands than in intact ones.

## 2. Study site

The study area was located in the western Harz Mountains in southern Lower Saxony, Germany. Two stands of Norway spruce (*Picea abies*) were selected on the Acker-Bruchberg ridge at an altitude of 790–820 m; thus, within the natural distribution range of Norway spruce in the Harz Mountains: a 149-year-old (in 1999) spruce stand heavily affected by forest dieback (stand “W” in Hauck and Runge, 1999) and a 160-year-old healthy or only slightly affected forest stand (stand “F”). The distance between these stands was 1 km.

Trees in the dieback-affected stand showed heavy needle loss. Many dead, standing trees were present. Damage has been apparent since the 1970s. Long-distance transport of acidic air pollutants is thought to be the general cause of spruce decline in the montane region of the Harz Mountains (Hauhs, 1985; Stock, 1990).

Similar pH and element content of incident precipitation in both stands were established during the vegetation period 1995 (Hauck and Runge, 1999) as well as in 1997–1998 (Hauck, 1999). However, soil pH differed significantly between the stands: the pH (KCl) was 2.89±0.42 in the A and 3.51±0.11 in the B horizon of the intact stand, and 2.31±0.15 in the A and 2.43±0.28 in the B horizon of the dieback-affected stand (Hauck, 1999). The extremely low soil pH of the dieback-affected stand could be a cause for the decline. If the deposition of acids has always been similar in both plots, then the buffer capacity of the soil in the damaged stand must have been lower. This is suggested by a peat layer in the latter stand, which is absent in the healthy one, where the soil is an oligotrophic pseudogley-brown earth. Alternatively, the deposition of acids in the damaged stand could have been higher in the past if the plot was more exposed to drifting clouds or fog. With advanced needle loss, this effect would have lost its significance. At present, we cannot decide between these alternatives, but in neither case would lichens be directly favored in the declining stand; on the contrary, they should be at a disadvantage. An influence of local pollution sources is improbable. A moderately frequented road is 150 m away from the declining plot and 1400 m from the intact one.

The climate of the Acker-Bruchberg area is characterized by a yearly precipitation of 1400–1500 mm and a yearly mean temperature of 4–5°C. Fog occurs on 130–200 days per year; a closed snow cover lasts 110–120 days per year (Glässer, 1994).

## 3. Materials and methods

### 3.1. Bark sampling and chemical analyses

Bark samples were collected from 50 spruce trees in the healthy stand and from 70 trees in the dieback-affected stand. Trees were selected by setting up $50\times10$ m plots. All trees within the plots with a minimum diameter of 15 cm and a height of at least 5 m were sampled. A preliminary test on 10 trees in each stand detected no decisive difference between the element content of bark from eastern and western exposure. Therefore, sampling was restricted to one standard exposure (i.e. western exposure at a height of 100–200 cm above the ground). 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. A water suspension of the pulverized bark (25 ml/g dry wt.) was used for measurements of pH and conductivity according to Müller (1981). In addition, exchangeable $H^+$ was measured after adding KCl to the suspension. Dry homogenates were taken for determinations of S, N, and C by infrared spectroscopy (S-Analyzer, Leco SC 132) and by gas chromatography (CN-Analyzer, Carlo Erba Strumentazione NA 1500). After acid digestion of homogenized bark, P was determined colorimetrically using the molybdenum-blue method (Allen et al., 1974). K, Ca, Mg, Fe, Mn, Al, Zn, Cu, and Pb were analyzed with an Atomic Absorption Spectrophotometer (Varian SpectrAA 30). Accuracy of the analytical methods was checked by analyzing a standard bark sample in 20 replicates. Precision of analysis was estimated by the coefficient of variation which was found to be (in %) 3.4 (N), 1.9 (P), 3.1 (S), 2.0 (C), 2.3 (K), 2.0 (Ca), 3.5 (Mg), 0.5 (Fe), 0.3 (Mn), 3.3 (Al), 0.2 (Zn), 5.1 (Pb), and 1.7 (Cu), respectively.

### 3.2. Vegetation mapping

Epiphytic lichen vegetation was mapped on each tree in a cylindric plot-segment comprising the western half of the tree trunk from 100–200 cm above the ground. Cover values of species were estimated in percent. For species identification, thin-layer chromatography was used where required (Culberson and Ammann, 1979). Nomenclature of lichens is based on Wirth (1994).

### 3.3. Statistics

Statistical calculations were made with the SAS 6.04 program (Schuemer et al., 1990; Gogolok et al., 1992). The significance of differences between samples was tested with the *U*-test of Mann–Whitney (Sachs, 1997), since the data were in general not normally distributed (according to the Shapiro–Wilk test). Spearman's rank correlation coefficient ($r_s$) and the non-linear correlation coefficient ($r_{\ln}$) were calculated according to Sachs (1997). Independent variables were rendered logarithmically before multiple regression analyses. Linear regression equations were calculated with help of the program Xact 4.01, SciLab Co, Hamburg.

## 4. Results

### 4.1. Element content of the substrate

Significant differences existed between the intact and the declining stand for all chemical parameters measured except C, P, and Al (Table 1). Mean content of S, K, Fe, Mn, Pb, Cu, and $\mathrm{H}^+$ as well as mean conductivity were higher in the intact stand than in the dieback-affected one. In contrast, the mean content of N, Ca, Mg, and Zn was higher in the dieback-affected stand than in the intact one.

### 4.2. Epiphytic lichen vegetation

A total of 21 lichen species was recorded from the areas of the tree trunks where the bark was sampled (Table 2). On average, 3.7±1.3 lichen species occurred in each relevé in the intact stand and 4.6±2.4 species in the dieback-affected stand ($P < 0.05$, *U*-test). In both stands, the lichen vegetation was dominated by *Lecanora conizaeoides*, however, its dominance was lower in the dieback-affected stand than in the intact one. Seven species had a significantly higher cover in the dieback-affected than in the intact stand, and three species had higher cover values in the intact stand.

### 4.3. Correlations between bark chemistry and cover of selected species

For investigating the correlations between element content of bark and lichen vegetation, cover values of the two most frequent lichen species, *Hypogymnia physodes* and *Lecanora conizaeoides*, were considered.

Cover of *Hypogymnia physodes* decreased non-linearly with increasing Fe, Mn, Al, and Cu content of bark in the dieback-affected stand and with Mn content in the intact stand. Correlation coefficients for these

Table 1
Element content of bark in the dieback-affected spruce stand compared to the healthy stand[a]

| | Healthy stand | | Dieback-affected stand | |
|---|---|---|---|---|
| | Arithmetic mean±S.D. | Median/interquartile range | Arithmetic mean±S.D. | Median/interquartile range |
| N [mmol/kg dry wt.] | 310.6±45.4 | 300.5/54.2 | 376.4±124.5*** | 336.7/112.9 |
| P [mmol/kg dry wt.] | 7.58±2.15 | 7.29/2.84 | 7.99±3.84 | 7.09/4.04 |
| S [mmol/kg dry wt.] | 18.96±2.50 | 18.82/2.78 | 16.89±6.05*** | 15.43/5.88 |
| C [mmol/kg dry wt.] | 43.96±0.95 | 43.97/0.68 | 44.17±0.83 | 44.09/0.96 |
| K [mmol/kg dry wt.] | 7.74±2.77 | 7.08/1.64 | 6.30±5.30*** | 4.83/2.01 |
| Ca [mmol/kg dry wt.] | 94.53±25.30 | 94.30/25.84 | 156.0±52.07*** | 147.2/73.4 |
| Mg [mmol/kg dry wt.] | 4.29±1.19 | 4.25/1.14 | 7.93±3.55*** | 6.96/3.58 |
| Fe [mmol/kgdry wt.] | 8.51±2.96 | 8.23/3.19 | 7.10±3.82** | 6.02/4.21 |
| Mn [mmol/kg dry wt.] | 1.86±0.70 | 1.68/0.78 | 1.66±0.90* | 1.41/1.00 |
| Al [mmol/kg dry wt.] | 6.66±2.46 | 6.31/2.56 | 6.28±3.44 | 5.76/3.51 |
| Zn [mmol/kg dry wt.] | 1.03±0.39 | 0.931/0.471 | 2.66±1.00*** | 2.66/1.37 |
| Pb [mmol/kg dry wt.] | 0.864±0.389 | 0.821/0.593 | 0.632±0.540*** | 0.490/0.581 |
| Cu [mmol/kg dry wt.] | 0.246±0.066 | 0.248/0.094 | 0.119±0.053*** | 0.109/0.064 |
| pH ($H_2O$) | 3.09±0.07 | 3.10/0.10 | 3.33±0.64*** | 3.29/0.14 |
| pH (KCl) | 2.95±0.08 | 2.96/0.10 | 3.24±0.13*** | 3.21/0.14 |
| Conductivity [µS/cm] | 367.8±50.5 | 360.0/55.0 | 283.2±55.2*** | 277.5/83.0 |

[a] Levels of significance: * $P \leqslant 0.05$; ** $P \leqslant 0.01$; *** $P \leqslant 0.001$ (*U*-test). Number of samples: *n* (Healthy stand) = 50; *n* (Dieback-affected stand) = 70.

Table 2
Epiphytic lichens on the sampled spruce trees[a]

| | Frequency (% sample trees) | | Mean cover (%) | | | Max. cover (%) | |
|---|---|---|---|---|---|---|---|
| | Healthy stand | Dieback-affected stand | Healthy stand | Dieback-affected stand | | Healthy stand | Dieback-affected stand |
| Species with higher cover in the dieback-affected stand | | | | | | | |
| *Cladonia pyxidata* s. l. | 0 | 11** | 0.00±0.00 | 0.06±0.20 | * | 0.0 | 1.0 |
| *Hypogymnia physodes* | 96 | 89 | 0.97±0.98 | 4.75±7.66 | ** | 4.5 | 41.0 |
| *Lecidea* cf. *hypopta* | 0 | 29*** | 0.00±0.00 | 0.27±0.79 | *** | 0.0 | 6.0 |
| *Mycoblastus fucatus* | 0 | 27*** | 0.00±0.00 | 0.63±2.72 | *** | 0.0 | 20.5 |
| *Parmeliopsis ambigua* | 12 | 74*** | 0.04±0.10 | 1.83±5.68 | *** | 0.3 | 39.0 |
| *Platismatia glauca* | 2 | 19** | 0.01±0.07 | 0.26±1.01 | *** | 0.5 | 7.5 |
| *Pseudevernia furfuracea* | 0 | 30*** | 0.00±0.00 | 0.36±1.06 | *** | 0.0 | 6.5 |
| Species with higher cover in the healthy stand | | | | | | | |
| *Cladonia digitata* | 24 | 3*** | 0.12±0.32 | 0.03±0.18 | *** | 2.0 | 1.5 |
| *Hypocenomyce caradocensis* | 66 | 0*** | 1.31±2.39 | 0.01±0.10 | *** | 13.0 | 0.8 |
| *Lecanora conizaeoides* | 100 | 100 | 54.60±13.07 | 17.43±15.11 | *** | 80.0 | 54.0 |
| Indifferent species | | | | | | | |
| *Chaenotheca ferruginea* | 4 | 0* | 0.01±0.06 | 0.00±0.00 | | 0.3 | 0.0 |
| *Cladonia polydactyla* | 16 | 24 | 0.06±0.13 | 0.24±0.63 | | 0.5 | 2.8 |
| *Hypocenomyce scalaris* | 4 | 0* | 0.01±0.06 | 0.00±0.00 | | 0.3 | 0.0 |
| *Hypogymnia tubulosa* | 0 | 1 | 0.00±0.00 | 0.04±0.30 | | 0.0 | 2.5 |
| *Lecanora symmicta* | 0 | 3 | 0.00±0.00 | 0.01±0.07 | | 0.0 | 0.5 |
| *Lepraria elobata* | 2 | 3 | 0.01±0.04 | 0.02±0.12 | | 0.3 | 1.0 |
| *Lepraria jackii* | 40 | 40 | 0.17±0.23 | 1.33±3.62 | | 1.0 | 20.0 |
| *Lepraria rigidula* | 0 | 6* | 0.00±0.00 | 0.03±0.12 | | 0.0 | 0.8 |
| *Parmeliopsis hyperopta* | 0 | 3 | 0.00±0.00 | 0.01±0.05 | | 0.0 | 0.3 |
| *Placynthiella icmalea* | 0 | 1 | 0.00±0.00 | 0.00±0.04 | | 0.0 | 0.3 |
| *Vulpicida pinastri* | 0 | 1 | 0.00±0.00 | 0.00±0.04 | | 0.0 | 0.3 |

[a] Data are calculated from relevés from the western half of the tree trunks from a height of 100–200 m above the ground. Frequency: presence in the relevés from the healthy stand ($n=50$) or the dieback-affected stand ($n=70$); statistics: $\chi^2$-test. Mean cover: arithmetic mean±S.D.; statistics: $U$-test. Levels of significance: * $P\leqslant 0.05$; ** $P\leqslant 0.01$; *** $P\leqslant 0.001$.

relationships, however, were rather low in these cases (Table 3). This was due to a high number of trees, which were not, or only very sparsely, inhabited by *Hypogymnia physodes*. Excluding all data with cover $\leqslant 1\%$ from the analysis resulted in higher correlation coefficients. Cover values versus bark content of the most closely correlated elements Mn and Cu are shown in Fig. 1. In the dieback-affected stand, multiple linear regression analysis using cover values $>1\%$ yielded $R=0.61$ ($P\leqslant 0.001$) if only Mn and Cu were included. The correlation coefficient was only slightly enhanced ($R=0.64$, $P\leqslant 0.01$), when Fe or Fe and Al, respectively, were additionally considered in the calculation.

Cover of *Lecanora conizaeoides* decreased non-linearly with increasing Mg and Mn content of bark in the dieback-affected stand but not in the intact one (Fig. 2). With increasing Cu content of bark, cover increased linearly in both stands. Correlation coefficients, however, were only $r_s=0.27$ ($P\leqslant 0.05$) in the dieback-affected and $r_s=0.31$ ($P\leqslant 0.05$) in the intact stand. No significant multiple regression model could be calculated with these variables.

Table 3
Univariate regression analysis for dependency of cover of *Hypogymnia physodes* on element content of bark[a]

| | All samples | | Samples with cover >1% | |
|---|---|---|---|---|
| | Healthy stand (d.f.=49) | Dieback-affected stand (d.f.=69) | Healthy stand (d.f.=12) | Dieback-affected stand (d.f.=36) |
| Mn | −0.36** | −0.26*(1) | −0.55* | −0.60* |
| Cu | n.s. | −0.39**(1) | n.s. | −0.51**(2) |
| Al | n.s. | −0.30* | n.s. | −0.46** |
| Fe | n.s. | −0.28* | n.s. | −0.45** |

[a] Non-linear correlation coefficients. Regression models: (1) $y=a+bx^c$, (2) $y=a+be^{cx}$; otherwise $y=a/(bx)$. Levels of significance: * $P\leqslant 0.05$; ** $P\leqslant 0.01$; *** $P\leqslant 0.001$; n.s., insignificant. Correlations with chemical species not mentioned here were insignificant.

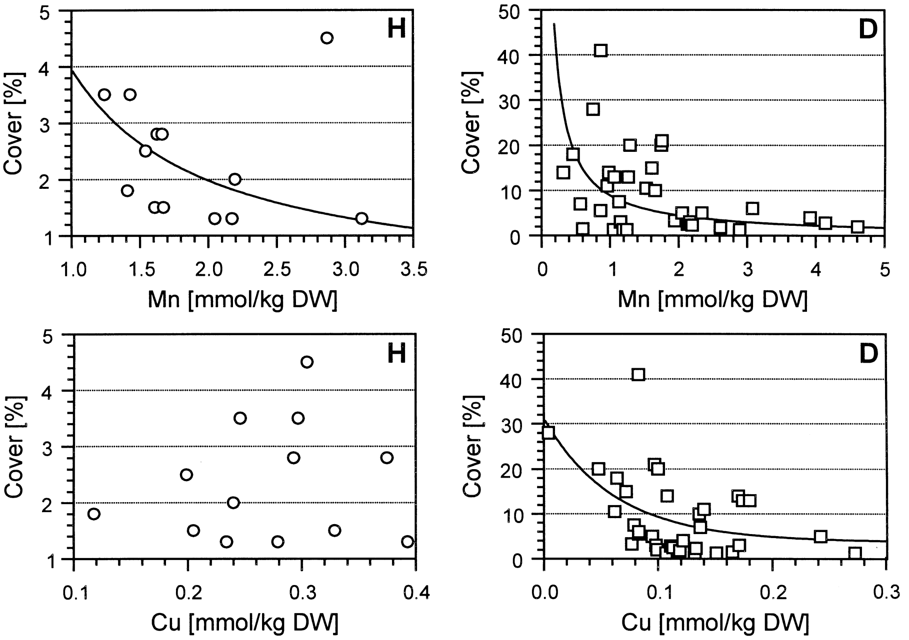

Fig. 1. Cover values >1% of *Hypogymnia physodes* versus Mn and Cu content of the substrate in the healthy (H) and the dieback-affected stand (D). The different scales in the diagrams should be noted.

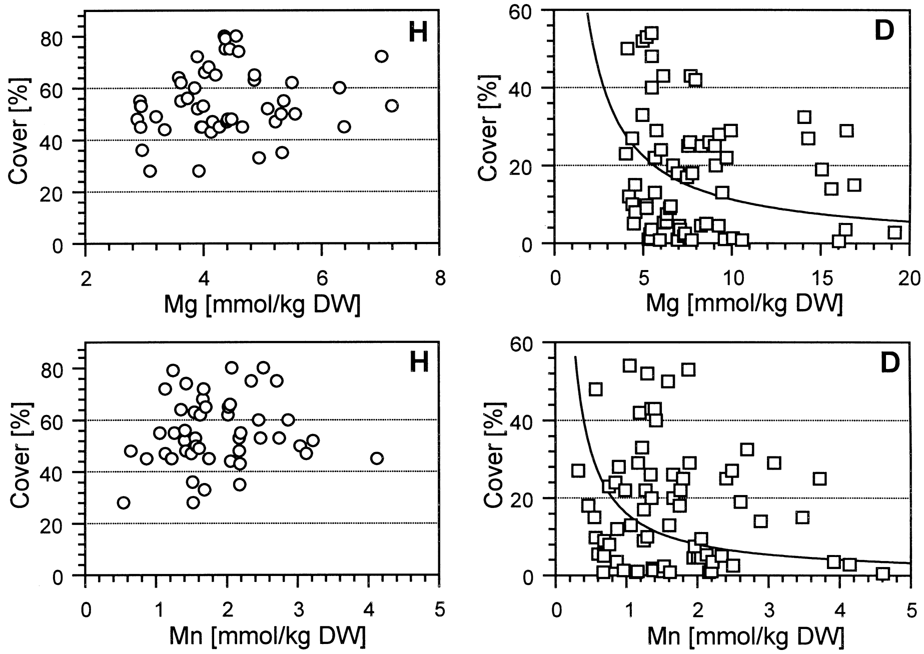

Fig. 2. Cover of *Lecanora conizaeoides* versus Mg and Mn content of the substrate in the healthy (H) and the dieback-affected stand (D). Correlations in D: $r_{\ln} = -0.37$, $P \leqslant 0.01$ (Mg); $r_{\ln} = -0.54$, $P \leqslant 0.001$ (Mn); regression model: $y = a/(bx)$. The different scales in the diagrams should be noted.

## 5. Discussion

### 5.1. Influence of forest dieback on the element content of bark

Lower content of S, K, Mn, and $H^+$ in bark of the declining stand compared to the intact one corresponds with lower content in stem flow that was measured in the declining stand by Hauck and Runge (1999). In these cases, therefore, differences in bark content seem to reflect differences in stem flow content.

The same applies to Fe. Hauck and Runge (1999) established Fe content in stem flow to be only insignificantly lower in the dieback-affected stand than the intact one; however, measurements during a longer period detected a significant difference (Hauck, 1999).

Pb and Cu could not be measured in stem flow because of concentrations below the detection limit of the AAS. Schmidt (1987), however, established the significance of atmospheric interception for the Pb and Cu status of the canopy in a stand of Norway spruce in Northern Germany. Pb emissions from a nearby road have apparently no substantial effect, as the Pb content is lower in the stand nearer the road than in the one located further away.

No relationships between bark content and stem flow content could be established in the case of N, Ca, Mg, and Zn. The content of these elements was higher in the bark of the declining stand, whereas the content in stem flow either did not differ significantly between the declining and the intact stand (N, Mg) or was even higher in the stem flow of the intact stand (Ca, Zn; Hauck and Runge, 1999). In order to explain these results, specific investigations must be performed. Liming can be ruled out as a cause of higher Ca and Mg content, as the declining plot has not been limed.

### 5.2. *Possible effects of bark chemistry on selected lichen species*

Univariate regression analysis gave weak but significant or even highly significant correlations between cover of *Hypogymnia physodes* and bark content of Mn, Cu, Fe, and Al in the declining stand (Table 3). Therefore, an influence of these elements on *Hypogymnia physodes* should be taken into consideration and will be discussed in the following.

Taking Mn and Cu as examples, it is apparent from Fig. 1 that univariate regressions are not well-suited models of the relationship between cover values found and element content of bark. At a given element content the cover varies between zero and a certain maximum, but remarkably, the maxima decrease with increasing element content. This distribution of the cover values suggests a multiple dependency in which the content of a certain element in the bark is one factor among others. Hauck and Runge (1999) established, for example, the S content of stem flow as affecting the cover of *Hypogymnia physodes*. However, from the relationship of maximal cover values and element content it appears that the latter can be the limiting factor in those cases in which other factors would have allowed higher values.

Correlations have been calculated separately for the intact and the declining stand. In the former, a significant correlation was established in the case of Mn only, but Fig. 1 shows that the same relationship can be assumed for both stands, as both sets of values fit into one another. In the intact stand a possibly limiting effect of the content of Cu does not become operative since another factor (e.g. light) sets the limit.

Only two experimental studies revealed a noxious effect of Mn to lichens. Exposure of *Cladonia rangiferina* to 10 and 100 mM of Mn, respectively, for 90 min resulted in slight $K^+$ losses. A significant loss of $K^+$ occurred only following an exposure to Mn concentration as high as 1 M, which exceeded considerably ambient levels (Burton et al., 1981). Goyal and Seaward (1982) established significant $K^+$ losses from *Peltigera canina* due to incubation with 2–16 mM of Mn. Current studies in our group showed that Mn concentrations found in the bark in the present study significantly affect the germination rate of soredia of *Hypogymnia physodes*. Mn (3 mM) reduced the germination rate by 82%. The maximum Mn content of bark was 4.2 mmol/kg dry wt. in the healthy and 4.6 mmol/kg dry wt. in the dieback-affected stand.

Cu toxicity to lichens has frequently been reported (Puckett, 1976; Branquinho et al., 1997; Tarhanen et al., 1999). In current unpublished studies of our group (Hauck, Zöller and Runge), we established that 0.24 mM of Cu reduced the germination rate of soredia of *Hypogymnia physodes* on agar plates by 48%. As *Hypogymnia physodes* rarely develops apothecia in the Harz Mountains, soredia germination is directly linked with cover values. Armstrong (1987) proved that most soredia of *Hypogymnia physodes* served for short-range dispersal within 2 cm from the source. Hence, even neighboring thalli can be supposed to originate from successfully germinated soredia and probably not from the dispersal of thallus fragments. Cu content in the bark of the dieback-affected stand achieved a maximum of 0.27 mmol/kg dry wt.

Fe and Al did not appear to affect the cover of *Hypogymnia physodes* (Table 3). Addition of Fe and Al to a regression model containing Mn and Cu did not result in a higher correlation coefficient, because both Fe and Al were strongly correlated with Cu (Fe: $r_s = 0.74$, $P < 0.001$; Al: $r_s = 0.73$, $P < 0.001$).

Distribution of *Lecanora conizaeoides* was considerably less affected by bark chemistry than that of *Hypogymnia physodes*. This was to be expected because *Lecanora conizaeoides* is known to be extremely toxitolerant (Wirth, 1985; Bates et al., 1996). Mn and Mg are the only elements that showed weak but significant correlations with the cover of this species. However, the content of these elements was correlated with each other in the declining stand ($r_s = 0.68$, $P \leqslant 0.001$). Thus, it is not clear which of these elements directly affected the cover of *Lecanora conizaeoides*. As *Lecanora conizaeoides* achieved high cover values on bark containing up to 11 mmol/kg dry wt. of Mn in other spruce stands studied by us (Hauck, 1999), a causal effect of Mn on *Lecanora conizaeoides* in the dieback-affected stand is improbable. Experimental studies on toxic effects of Mg on *Lecanora conizaeoides* are lacking, but such effects cannot be ruled out, as the species is an extreme acidophyte (Wirth, 1985). The increasing cover of *Lecanora conizaeoides* with increasing Cu content of the substrate agrees with the known toxitolerance of the species.

Despite its close correlation with *Hypogymnia physodes* and *Lecanora conizaeoides* in stem flow (Hauck, 1999), S had no effect when its content in bark was considered. This may indicate that the lichen thalli take up S mainly from stem flow and not from the substrate.

## 6. Conclusions

Our measurements confirm the hypothesis that the element content of bark in dieback-affected montane spruce forests is different from that in comparable healthy stands. Bark content of those elements which occur in lower amounts in the dieback-affected stand than in the intact one is apparently primarily affected by stem flow. Thus, needle loss has two effects on the chemical conditions on the trunk surface: a modification of the element content of stem flow as proven by Hauck and Runge (1999) and a modification of the element content of the bark caused by the changes in stem flow chemistry. Correlations, found between the cover of selected lichen species and the element content of the substrate, support our hypothesis that chemical site conditions are decisive for the high epiphytic lichen diversity in dieback-affected montane spruce forests of Central Europe.

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