Site factors determining epiphytic lichen distribution in a dieback-affected spruce-fir forest on Whiteface Mountain, New York

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Michaela Schmull
aus Kiel

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Referent: Prof. Dr. Michael Runge

Korreferent: Prof. Dr. Stephan Robbert Gradstein

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1 Introduction

Epiphytic lichens are considered to be particularly sensitive to environmental parameters, such as elevation, exposure, and inclination (natural factors) as well as pollution (anthropogenic impact). Since the beginning of the 1980s causes of lichen distribution have been discussed repeatedly, as an increase in lichen diversity with declining tree vitality due to pollution effects was observed in several areas in Germany (MÜLLER 1983, KÖSTNER & LANGE 1986, BARTHOLMESS 1989, GLIEMEROTH 1990, MACHER 1992, HAUCK & RUNGE 1999). Most lichenologists held the microclimate (i.e. higher light influx and increased water-holding capacity of the bark on declining trees) responsible for the increased lichen diversity (e.g. JOHN 1986, MACHER & STEUBING 1986). However, investigations carried out in the Harz Mountains, Germany, by HAUCK (2000) and HESSE (2002) indicated that chemical site factors are decisive for lichen frequency. Needle loss in dieback-affected coniferous forests led to a reduced pollutant load on the trunk surfaces and enabled a more diverse epiphytic lichen vegetation than in healthy forest stands with identical atmospheric input of pollutants. The strongest impact had the S concentration measured in the stem flow on the decreasing cover of epiphytes.

In the early 1980s, at about the same time when forest decline was most extensively studied in Germany, an increasing mortality of *Picea rubens* on the mountains in the northeastern U.S.A. was noticed. Since then, numerous studies were carried out on Whiteface Mountain, New York. Whiteface Mountain is, similar to the study area in the Harz Mountains, characterized by coniferous forests, forest decline due to airborne chemicals, and high precipitation, whereas on the other hand fundamental differences distinguish the two areas:

(1) Two tree species are dominating the forest belt above 900 m elevation on Whiteface Mountain (*Abies balsamea* and *Picea rubens*), whereas in the Harz Mountains only *Picea abies* occurs.
(2) Only *Picea rubens* was found to be affected on Whiteface Mountain over 900 m elevation by airborne chemicals, mostly S compounds, whereas *Abies balsamea* remained unaffected (SCOTT et al. 1984, PEART et al. 1991, JOHNSON 1992, EAGER & ADAMS 1993).
(3) Element concentrations in the incident precipitation are lower on Whiteface Mountain as compared to the Harz Mountains (National Atmospheric Deposition Program, HAUCK 2000).
(4) The epiphytic lichen flora differs between Central Europe and North America.

In order to clarify whether chemical site factors are affecting lichen distribution under different biotic and abiotic conditions as compared to the Harz Mountains, a project on Whiteface Mountain was conducted.

For the present study it was hypothesized that:

(A) the lichen frequency on dead trees is higher compared to living trees,
(B) the lichen frequency on fir is higher compared to spruce,
(C) the chemical parameters of stem flow and bark are of decisive importance for lichen distribution,
(D) the microclimate is of minor importance.

Therefore, lichen vegetation was mapped on dead and living trees of each *Abies balsamea* and *Picea rubens* and stem flow samples as well as bark samples were collected and analyzed for their element concentrations in the present thesis. In addition, microclimate measurements were carried out by HOFMANN (2001) at the same field site; essential results of this study are also compiled in the present study.

2 Study area

2.1 Location

The study area is located on Whiteface Mountain in the Adirondacks, Essex Co., New York State, U.S.A. The Adirondacks are a mountainous region, approximately 200 km in diameter in northern New York State. Whiteface Mountain (1483 m elevation) is located in the northeastern part of Adirondack State Park. Data were collected on the northwestern slope of Mt. Esther, one of the lower peaks of Whiteface Mountain (1292 m elevation, 44°23'23'' N and 73°53'76'' W) at 1100 m in a stand dominated by balsam fir (*Abies balsamea* [L.] Mill.) and red spruce (*Picea rubens* Sarg.). The oldest spruce trees are up to 300 years old in that part of the mountain (JOHNSON 1987). *Abies balsamea* and *Picea rubens* were intermixed with paper birch (*Betula papyrifera* Marsh.) and rarely American mountain ash (*Sorbus americana* Marsh.). Young growth was dominated by *Abies balsamea*.

2.2 Geology

The region of the Adirondack Mountains can be divided into the Central Highlands and the Northwest Lowlands, separated by the Carthage-Colton Mylonite Zone (ISACHSEN et al. 1991). The highest elevations are found in the High Peaks of the Central Highlands, where numerous summits rise above 1200 m. Mount Marcy, the highest peak, is 1629 m high.

The rocks of the Adirondacks have been strongly folded and sheared by ductile deformation and shattered by brittle deformation (ISACHSEN et al. 1991). They are almost without exception metamorphic and Middle Proterozoic in age. Most of the rocks in the Northwest Lowlands are metasedimentary or metavolcanic and deposited in shallow seas beginning about 1.3 billion years ago. The rocks of the Central Highlands, where granitic gneiss is the most common, are metaplutonic (ISACHSEN et al. 1991). Metanorthosite also forms several large bodies in the Highlands; the highest are the High Peaks area. Olivine metagabbro bodies are scattered throughout the eastern and southeastern Adirondacks. Most of the metaplutonic rocks, including the metanorthosite, granitic gneiss, and olivine metagabbro bodies were formed from magmas that were intruded about 1.15 to 1.10 billion years ago (ISACHSEN et al. 1991).

On Whiteface Mountain one can find in addition to metamorphosed rocks of uncertain origin, which are mostly quartz-feldspar gneisses, also the metamorphosed igneous rocks (metanorthosite; WITTY 1968, FISHER et al. 1980, ISACHSEN et al. 1991). The latter one is the dominant bedrock of Mt. Esther and the bedrock of the field site. According to JOHNSON et al. (1994) cryorthods are the most common soil types.

2.3 Climate

Whiteface Mountain is located in the Northern Plateau climatic division of New York State, which encompasses the entire Adirondack region. MORDOFF (1949) describes the Plateau division as presenting an almost typical continental type of climate. The mean annual temperature at 603 m elevation on Whiteface Mountain is 6.2 °C with a maximum of 19.8 °C in July and a minimum of -8.3 °C in January (Atmospheric Sciences Research Center, unpubl.). The average length of the growing season is less than 105 days. The average annual precipitation is 1100 mm (National Atmospheric Deposition Program, unpubl.), with a summer maximum of 110 mm in August (Atmospheric Sciences Research Center, unpubl.). Clouds extend as low as 1000 m for 15 % of the year (MOHNEN 1989). The prevailing winds are westerly, modified by topography and persistence (WITTY 1968).

2.4 History and forest vegetation

Pulp cutting began in 1882 on the east of Whiteface Mountain and ceased before 1900 (NICHOLSON 1965). There have been several wildfires on the mountain, but apparently none since 1915. Since then, vegetation has remained intact except for the small amount cut for making ski trails and roads (WITTY 1968). The Adirondack region and especially Whiteface Mountain have been popular for tourism for more than a century because of the spectacular view from its summits. Trails were blazed on Whiteface for hikers and excursions on horseback (STODDARD 1881, DONALDSON 1921). The Whiteface Memorial Highway up to the summit was completed in 1934 and since then tourists can visit the summit by car. Whiteface Mountain is a part of the Adirondack Forest Preserve established by law in 1883, which prohibited further sale of state lands (MULHOLLAND 1932). This precludes the use of the land for all except recreational and watershed uses by the public.

Forest vegetation on Whiteface Mountain changes with elevation. Up to 650 m *Acer saccharum* Marsh., *A. rubrum* L., *Betula alleghaniensis* C.E. Britton, *B. papyrifera*, *Fagus grandifolia* Ehrh., *Pinus resinosa* Ait., *P. strobus* L., and *Quercus rubra* L. are the dominant tree species (WITTY 1968). Between 800 and 1100 m the most common tree species are *Abies balsamea*, *Picea rubens*, and *Betula papyrifera*. The summit area is above tree line; stunted *Abies balsamea* occur a few vertical feet below the summit in protected areas (WITTY 1968).

The area of the sample plot has always been unused. Timber was probably never harvested and tourism never took place on the field site.

2.5 Forest dieback

Between the mid-1960s and mid-1980s, red spruce died at unusual rates on the mountains of upstate New York and western New England. In the live red spruce basal area over 900 m elevation, red spruce declined 71 % at Whiteface Mountain (SCOTT et al. 1984, PEART et al. 1991, JOHNSON 1992). At elevations below cloudbase in hardwood-dominated stands (> ca. 850 m), red spruce mortality was apparently much lower than at higher elevations (SILVER et al. 1991). Changes in crown condition, growth, and foliar symptoms have been observed. Deterioration of crowns affected shoot and diameter growth (LEBLANC & RAYNAL 1990). Variations in internode length were recorded, with trees showing the greatest of dieback and the most brooming having the shortest shoot extension and greatest reduction in diameter growth (JOHNSON 1992). Diameter and volume growth of *Picea rubens* decreased sharply across the northeast after 1955-1960 without recovery by the mid-1980s (JOHNSON & SICCAMA 1983, COOK et al. 1987, CRAIG & FRIEDLAND 1991). Needle symptoms such as intermittent mottling, flecking, whole-needle chlorosis and necrosis, necrotic or chlorotic tips (MILLER-WEEKS & COOKE 1989, PEART et al. 1991, BOYCE 1995) have been observed. Hypotheses that extremes in winter temperature, high winds, drought, insects, and fungal pathogens as well as solar radiation were important stresses in the deterioration of red spruce condition have been investigated (TEGETHOFF 1964, KELSO 1965, WHEELER 1965, RIZZO & HARRINGTON 1988, BUSING & PAULEY 1994, BOYCE 1995). Further, the possibility of Al toxicity to roots resulting from acid deposition was asserted (SCHLEGEL et al. 1992) as studies of cap cloud chemistry found an average summertime pH of 3.5, arising primarily from SO_4^{2-} ions (MOHNEN 1989). Additionally, ozone concentrations at elevations of over 900 m averaged 47 ppb daily during the growing season and did not show the diurnal pattern typical of lower elevations (MOHNEN 1989). Some of these hypotheses have been generally accepted, but according to JOHNSON (1992) evidence clearly indicates a role for airborne chemicals. Atmospheric S deposition reduced the cold tolerance of red spruce due to denaturation of proteins, membrane damage, increased assimilate consumption, inhibition of photosynthesis and leaching of cations (EAGER & ADAMS 1993). *Abies balsamea* is not affected by acidic precipitation and, thus, balsam fir dominates young growth.

3 Methods

3.1 Selection of sample trees

A 100 x 100 m sample plot was selected. In this plot, all *Abies balsamea* and *Picea rubens* trees with a diameter at breast height of at least 15 cm and a height of more than 5 m were recorded, marked and divided into living and dead sample trees. 27 trees of each species (*Abies balsamea*, *Picea rubens*) and variant (living, dead) were randomly selected for bark analyses. 10 additional trees of each type were selected for stem flow sampling. 37 living spruce trees were available in the plot.

3.2 Estimation of tree vitality

For the investigated trees, the cover of the crowns (Tab. 3-1) was estimated, using a scale with five classes according to HAUCK (2000). Living trees with a cover of the tree crown from 76 to 100 % were classified as vitality class V, whereas dead trees were grouped into class I. Classes II to IV were intermediate stages (Tab. 3-1). This method requires less experience for estimating the phorophyte vitality, compared to the popular method of determination of needle loss (HANISCH & KILZ 1990), where one has to know the optimum foliation in order to estimate needle loss. According to ELLENBERG (1996) needle mass varies even between living trees due to different climatic and edaphic habitat conditions.

For precipitation studies a total of 40 trees was selected (Ch. 3.1). According to the classification of tree vitality, all dead trees, - independent of the genus -, belonged to vitality class I. All living fir were listed in class V, whereas eight trees of living spruce belonged to vitality class V and two trees to class IV.

Bark properties were studied on 27 trees each of living spruce, dead spruce, living fir, and dead fir. Fifteen trees of the living fir were grouped into class V, six trees into class IV as well as four and one tree into vitality classes III and II, respectively. Fourteen trees of the living spruce belonged to class V, six trees to class IV, five trees to class III and two trees to class II. All dead trees belonged to vitality class I.

Tab. 3-1. Scale for estimation of tree vitality (HAUCK 2000).

Vitality class	Definition
I	Dead trees (needles absent)
II	Needles present; cover of tree crown 1 – 25 %
III	Needles present; cover of tree crown 26 – 50 %
IV	Needles present; cover of tree crown 51 – 75 %
V	Needles present; cover of tree crown 76 – 100 %

3.3 Vegetation mapping

Each trunk of the trees selected for bark sampling was divided into two plots (NW, SW). The vegetation was mapped by estimating the cover in percent of each epiphytic lichen species on both plots of each trunk in a height from 100 to 200 cm above soil level. For species identification, samples were taken for microscopic determination, and thin-layer chromatography was used if necessary (CULBERSON & AMMANN 1979).

The trunk of each tree selected for the precipitation studies was divided into four plots (NW, NE, SW, SE) and divided into 0 – 100 cm and 100 – 200 cm sections. Lichen vegetation was mapped in each of these eight relevés as described above. The relevés of a given trunk were combined into a single relevé for data analysis. This method provided mistakes of estimation which could have occurred by estimating cover on a bigger section of the trunk surface.

The nomenclature of the lichen taxa is based on ESSLINGER & EGAN (1995). Exceptions are *Lepraria jackii* (TØNSBERG 1992), *Micarea botryoides* (HAWKSWORTH et al. 1980) and *Parmeliopsis capitata* (HINDS & HINDS 1998). *Cladonia macilenta* and *C. pyxidata* are used in a wide circumscription including *C. bacillaris* and *C. floerkeana* in the former case and *C. chlorophaea* as well as *C. grayi* and allied chemospecies in the latter case (WIRTH 1995). *Usnea* was only identified on the generic level. When growth forms of the epiphytes were discussed in the present study, the pendulous form (i.e. *Alectoria*, *Bryoria*, and *Usnea*) was separated from fruticose lichens. Thus, the term fruticose lichens as used in the present study means fruticose lichens except for the pendulous ones. Lichens were further divided into crustose and foliose growth forms.

3.4 Precipitation studies

3.4.1 Sampling of stem flow and incident precipitation

Precipitation was sampled weekly over two vegetation periods. Measurements in 1999 (15 weeks) and 2000 (16 weeks) started in June and lasted until September.

Stem flow was collected weekly in 4 l polythene bottles on 10 living trees of *Abies balsamea* (B), 10 dead *Abies balsamea* (DB), 10 living *Picea rubens* (R) and 10 dead *Picea rubens* (DR) using polyurethane circular gutters (MEIWES et al. 1984). In fall 1999, one living tree of *Abies balsamea* was damaged by Hurricane Floyd and thus could not be sampled in 2000.

Incident precipitation was collected near the Whiteface Mountain toll road at 1200 m and 1000 m altitude. A third station was established in the first year on a small clearing very close to the sample plot at 1100 m. Significantly higher element concentrations than in the samples from the two other sample stations, however, showed that the clearing was too small for the sampled precipitation to be unaffected by the canopy. Thus, this station was given up.

Incident precipitation was collected in triplicate 1 l polythene bottles at 1 m above the ground. The total collecting surface of Büchner funnels attached to the bottles was 78.5 cm^2.

3.4.2 Sample preparation and chemical analysis

Water samples were filtered with ash-free filters (Schleicher & Schuell, Blue Ribbon Filters) and pH (Orion Research Digital pH/millivolt Meter 611, electrode: Orion 8103 Ross Combination pH) and conductivity (YSI, 34 Conductivity Resistance Meter) were determined. For preservation a drop of 300 µM phenylmercuric acetate solution (PMA) was added to each sample. The solutions were stored at 4 °C until further analysis. Samples were analysed for P, S, K, Na, Ca, Mg, Fe, Mn, Al, Zn, and Cu by Inductively Coupled Plasma Atomic Emission Spectrometry (ICP-AES, Perkin Elmer, Plasma 400 Emission Spectrometer). NH_4^+ and NO_3^- were measured colorimetrically with an Auto-Analyzer (Alpkem, 240). For determination of NO_3^-, NO_3^- was reduced to NO_2^- in a Cd-Cu column. After reaction with sulfanilamide, NO_2^- was measured by forming an azo dye with N-(1-naphtyl)ethylenediamine dichydrochloride. NH_4^+ was determined in a complex with indophenol blue.

3.5 Substrate studies

3.5.1 Sampling

Bark samples were taken from the west sides of the tree trunks (150 ± 50 cm above soil level) after mapping the lichen vegetation (bark sample trees). Bark was collected with a knife and afterwards cleaned from epiphytes with a tooth brush. Pieces with large amounts of resin as well as wood were removed. Sampling was restricted to dead bark tissue.

Bark samples were also taken from the stem flow trees after stem flow sampling was finished in fall 2000.

3.5.2 Chemical analysis

3.5.2.1 Total element content of bark

Bark samples of the bark sample trees were dried at 105 °C and homogenized with an agate mill. Conductivity and pH (H_2O and KCl) were measured in a water suspension (25 ml g^{-1} DW; MÜLLER 1981). After measuring the pH (H_2O), KCl was added and re-measured after half an hour (pH [KCl]).

Dried bark homogenate was acid-digested with 65 % HNO_3 under pressure and analysed for K, Ca, Mg, Fe, Mn, Zn, Pb, and Cu by atomic absorption spectrophotometry (AAS; Varian, SpectrAA 30). C and N were determined gas chromatographically (CN-Analyzer Carlo Erba Strumentazione NA 1500).

3.5.2.2 Comparison of different extractants

1.5 g of dried and ground bark homogenate of each sample of the stem flow trees was taken and shaken for 2 hours in deionized H_2O, 25 mM EDTA, and 25 mM $SrCl_2$, respectively. After centrifugation at 9000 rpm for 10 min and filtering with membrane filters (GN-6 Metricel®, Pall GelmanSciences) all samples were analysed with the ICP-AES for K, Ca, Mg, Fe, Mn, Zn, and Cu.

To investigate the potential influence of bark element content on lichen cover, the established method of determining total element content and correlating lichen cover against element content was used. However, lichens growing on the trunk of a tree are never exposed to total amounts of elements in the bark. Thus, a method was chosen where different extractants were checked for their effectiveness in dissolving elements out of the bark. The selected extractants in this study were H_2O, EDTA, and $SrCl_2$. H_2O was the media where it was most likely that the contents dissolved from the bark present the concentrations to which the lichen on the trunk of the tree is exposed. EDTA and $SrCl_2$ were, in that order, stronger extractants. No prior investigations have been made referring to this from other working groups.

3.5.2.3 Electron microscopy and X-ray microanalysis

Cross sections of bark (2.5 mm length) and pieces of resin were cut out of a trunk of *Abies balsamea*, rapidly frozen with liquid nitrogen in a 1:3 mixture of propane:isopentane at –196 °C (JEHL et al. 1981), freeze-dried at –50 °C (Piatkowsky, P4K-S) and stored over silica gel. After carbon-coating, the samples were analysed for Mn with a scanning electron microscope (SEM; Philips, SEM 515) by using energy dispersive X-ray microanalysis (EDAX 9100).

Additionally, sections of the same bark were pressure-infiltrated with diethyl ether under vacuum after freeze-drying, then successively embedded in styrene-methacrylate (FRITZ 1989) and encapsulated. One µm thick sections were cut with an ultramicrotome using dry glass knives, mounted on adhesive-coated 100-mesh hexagonal copper grids (FRITZ 1991), coated with carbon and stored over silica gel until further analysis. The sections were analysed for Mn in a transmission electron microscope (TEM; Philips, EM 420) with the energy dispersive system EDAX DX-4. Different cellular tissue of the bark as well as tissue compartments of cell walls (primary and secondary cell walls), and lumina were analysed separately under water-free conditions. Quantitative data in mmol dm^{-3} were obtained by comparing peak integrals of the elements with K peaks of standards containing known amounts of K (FRITZ & JENTSCHKE 1994), taking into account the calibration coefficients (CLIFF & LORIMER 1975) of the elements relative to K.

3.5.3 Determination of water-holding capacity

Data for water-holding capacity and microclimate measurements (except for two of the three light measurements on all bark and stem flow sample trees, Ch. 3.6) presented in this thesis are based on the Diplomarbeit of HOFMANN (2001).

60 trees (15 each of living and dead fir as well as living and dead spruce) were randomly selected out of the 108 bark sample trees (Ch. 3.1). Pieces of bark with a maximum diameter of 3 cm were soaked in 200 ml of deionized H_2O for 24 h. After removing the free water with a paper towel the samples were dried at 105 °C for 24 h and the water-holding capacity determined by calculating the wet minus the dry weight and specifying the result as percentage water content related to dry weight (HAUCK et al. 2000).

3.6 Microclimate measurements

3.6.1 Light measurements

On 12 days with complete cloud cover the photosynthetic photon flux density (PPFD) of photosynthetically active radiation (PAR) was measured on 60 randomly selected trees out of the 108 bark sample trees described in Ch. 3.1 at a wavelength of 400 to 700 nm (PAR sensor Licor, LI-190SA and Licor datalogger, LI-1000). Sensors were held 150 cm above ground within 10 cm of the trunk surface in a horizontal position adjusted with a spirit level. Simultaneously, the radiation was determined on a clearing near the Whiteface Mountain toll road. Three measurement readings per minute were taken. The means of the measurements were specified as percentage light content related to the mean of the radiation above canopy at the same minute.

At 3 days the radiation was determined for bark and stem flow sample trees (n = 99).

3.6.2 Determination of evaporation

Evaporation was determined with Piche evaporimeters (STOUTJESDIJK & BARKMAN 1992) on the 60 randomly selected trees out of the bark sample trees described in Ch. 3.1. With this method, a green filter paper (3 cm in diameter) is supposed to imitate a deciduous leaf (STEUBING & FANGMEIER 1992). The evaporimeter was filled with deionized H_2O, sealed with the filter paper and hung upside down on the tree at 150 cm above ground in western exposure. The amount of evaporated water was recorded daily between 17.00 and 18.00 o'clock for four weeks (04.08. – 03.09.00).

3.6.3 Diurnal variation of relative humidity, temperature and evaporation

Measurements of relative humidity, air temperature, and evaporation were carried out on the 60 randomly selected trees out of 108 bark sample trees described in Ch. 3.1 on 5 – 6 days, beginning shortly before direct insolation of the northwest facing slope of the sample plot at 8.15 in the morning and ending at 6.45 in the evening. Air humidity and temperature were determined hourly with an Assmann psychrometer subsequent to an adjustment time of 3 min after the aspirator was wound up (STOUTJESDIJK & BARKMAN 1992). The psychrometer was held 150 cm above ground and 2 cm in front of the trunk. The evaporation was measured hourly as described in Ch. 3.6.2.

3.7 Experimental studies to the NO_3^- sensitivity of *Hypogymnia physodes*

3.7.1 Chlorophyll content

Thalli of *Hypogymnia physodes*, sampled from *Picea abies* in the Lüneburger Heide (south of Kreisstraße 17, approximately 20 km southwest of Uelzen, between Unterlüß and Lutterloh, Lower Saxony, Germany) were cultivated on moist filter paper in Petri dishes in growth chambers for one week at 80 % relative humidity, at a light intensity of 30 µmol m^{-2} s^{-1} and a daily temperature of 13 °C (13 hours per day); night temperature was 10 °C. The region of the Lüneburger Heide was chosen as a sample site because it is an overall low-polluted area, where it was likely that *Hypogymnia physodes* did not show any pre-damage. *Hypogymnia physodes* is a common species in Germany as well as on Whiteface Mountain and was used as a model organism in previous studies of our working group.

Ten replicates each were shaken for 1 hour twice a day in 60 ml of each of the following $NaNO_3^-$ solutions: 0 µM, 100 µM, 1 mM, and 10 mM at pH 4, where pH 4 corresponds to the pH measured in the stem flow on Whiteface Mountain. One hundred µM was the highest concentration found in stem flow from Whiteface Mountain; 1 mM was the maximum concentration found in the stem flow from the study sites of our group in Germany (Harz Mountains); 10 mM was an excess concentration. An additional control (0 µM NO_3^-) with pH 6 was used in order to exclude the possibility that the low pH of 4 was the reason of possible damage. At the end of the experiment three pieces, each of 0.26 cm^2 were removed from the thallus of each replicate and weighed under water-saturated conditions. Three ml N,N-dimethyl formamide (DMF) were added to each of the replicates and incubated at 4 °C for 24 hours (MORAN 1982). The absorption of the extractions was measured colorimetrically (Shimadzu, UV-160) at λ = 603, 625, 647, and 664 nm for determination of the chlorophyll content. The chlorophyll a- and chlorophyll b-contents were calculated according to MORAN (1982):

$$\text{Chl a [ppm]} = 12.81\ A_{664} - 2.16\ A_{647} - 1.44\ A_{625} - 4.91\ A_{603};$$
$$\text{Chl b [ppm]} = -4.93\ A_{664} - 26.01\ A_{647} + 3.74\ A_{625} - 15.55\ A_{603}.$$

By adding 5 N HCl to the chlorophyll extracts and a second incubation for 1 hour the phaeophytin a- and phaeophytin b-contents were colorimetrically determined after Moran (1982) at λ = 654 and 666 nm and calculated with the following equation:

Phaeo a' [ppm] = 23.91 A_{666} – 7.22 A_{654};
Phaeo b' [ppm] = 16.38 A_{666} + 37.41 A_{654}.

3.7.2 Electron microscopy

Sections of the lichen thalli treated with the different NO_3^- solutions described in Ch. 3.7.1 were freeze-dried and coated with gold (SC 500, emscope). Different parts of the lichen thalli (i.e. soredia, upper cortex, medulla, algal layer, and cross sections of the thallus) were investigated with SEM for structural changes caused by the NO_3^- treatment.

3.7.3 Ergosterol content

Thallus pieces (100 mg) of the lichens treated with the different NO_3^- solutions described in Ch. 3.7.1 were used for determining the ergosterol content in order to test the influence of the NO_3^- treatment on the fungal partner of the lichen. Ergosterol is a sterol primarily located in the membranes of fungi (WEETE 1973, ELIX 1996). Just in few algae this sterol was found (e.g. *Chlorella* spp.; GOODWIN 1974). However, *Trebouxia* spec., the algal component of *Hypogymnia physodes*, synthesized ergost-5-enol, clionasterol, and poriferasterol when cultured alone but not ergosterol. Ergosterol is used as a marker of living fungal biomass because of its rapid turnover in dead cells (GRANT & WEST 1986).

Air dried lichen thalli of each replicate were ground and freeze-dried. Samples were weighed and hydrolysed with 6 ml 10 % KOH in methanol and 900 µM 2,6-di-*tert*-butyl-*p*-cresol (BHT; antioxidant) for 2 hours at 60 °C. After centrifugation (at 1000 rpm for 5 min), 4 ml of the cooled supernatant was removed and 2 ml each of n-hexane and deionized H_2O were added. The samples were shaken for 5 min and re-centrifuged. One ml of the organic phase was transferred into vials and ablated in a vacuum chamber. The residue was liquefied in 300 µl methanol and frozen until further analysis with a high performance liquid chromatograph (HPLC) with a LiChrospher®-100 column (Merck).

3.8 Soil analysis

Soil samples were taken at 20 randomly selected spots of the field site and collections were made separately from the organic layer (O_f) and the A horizon after recording soil properties. Soil was air dried and suspensions of 10 g DW of soil in 20 ml of deionized water were used to determine the pH (H_2O and KCl). C and N were analysed using gas chromatography. Air dried mineral soil was sieved and used for soil extractions with 0.1 M $BaCl_2$ for 12 hours. The organic matter (O_f) was digested with HCl after sieving. Then, 0.5 g of organic soil was weighed into porcelain crucibles and ashed at 500 °C for 12 hours. After dissolving each sample in 5 ml 5 N HCl, the crucibles were heated for 1 hour at 115 °C and diluted to a 1 N solution. Concentrations of the elements K, Ca, Mg, Fe, Mn, Al, and Zn were analysed in the samples both from mineral soil and the organic layer.

3.9 Statistics

Data were statistically processed with the program SAS 6.04 (SCHUEMER et al. 1990, GOGOLOK et al. 1992). Normal distribution of all data was tested with the Shapiro-Wilk test. When data were normally distributed, the t-test was used for testing the significance of differences between mean values of two samples; otherwise the U-test was used. The significance of differences between frequencies was tested with the χ^2-test. Correlations were calculated according to SACHS (1997), confidence limits according to BORTZ (1999). Pearson's product-moment correlation coefficient was used for describing linear relationships of binormally distributed data, whereas Spearman's rank correlation coefficient was used in the case of non-binormally distributed data. R stands for the multiple correlation coefficient that describes the dependency of Y on the variables A and B. Multiple regressions with more than one independent variable were computed with the 'REG' procedure of the SAS program. The independent variables were selected with help of 'RSQUARE' command first. The 'ANOVA' and the 'GLM' procedure were used for analyses of variance. Regression equations were calculated with the program Xact 4.01, SciLab Co.

Arithmetic means and their standard deviations (connected with '±') are quoted. Referring to SACHS (1997), the standard deviation was calculated even when the data did not follow the Gaussian distribution. In addition to mean value and standard deviation, minimum, maximum, median, and range are given in several cases.

4 Results

4.1 Lichen vegetation

4.1.1 Influence of tree species on epiphytic lichen vegetation

51 lichen species were found on the investigated fir and spruce trees. 40 lichen species grew on living *Abies balsamea*, 35 grew on living *Picea rubens*, 38 on dead *A. balsamea*, and 40 on dead *P. rubens*. Total mean cover of all lichen species together was higher on living *Abies balsamea* than on living *Picea rubens* (U-test, $p \leq 0.001$), whereas the dead trees did not show any differences. More taxa with higher mean cover and larger variation of cover were found on dead and living *Abies balsamea* compared to their counterparts on *Picea rubens* (Tab. 4-1, for detailed species list see Tab. 4-A1 - 4-A2, Tab. 4-A3). The same was true for the total of lichen species with a mean cover > 1 % (Tab. 4-1, for detailed species list see Tab. 4-A1 - 4-A2), and for the number of lichens with a higher constancy (Tab. 4-1, for detailed species list see Tab. 4-A4 - 4-A5). The most common lichen on each type of tree was *Arthonia caesia* (Tab. 4-A1 - 4-A2), except for dead *Abies balsamea*, where *Hypogymnia physodes* was dominating (Tab. 4-A2). 75 % (30 taxa) of the lichen taxa growing on living *Abies balsamea* and 80 % (28 taxa) on living *Picea rubens* never exceeded a mean cover of 1 % (for dead fir and spruce see Ch. 4.1.2). Most epiphytic lichens occurred on both tree species, but some were restricted to one of the phorophyte species such as *Calicium glaucellum*, and *Hypocenomyce scalaris* on *Picea rubens* as well as *Everniastrum catawbiense*, *Graphis scripta*, *Hypogymnia tubulosa*, *Lecanora pulicaris*, *Loxospora elatina*, and *Ropalospora chlorantha* on *Abies balsamea*.

Tab. 4-1. Number of lichen taxa in a comparison of living *Abies balsamea* (B) and living *Picea rubens* (R) as well as dead *A. balsamea* (DB) and dead *P. rubens* (DR). n = 37.

	Lichens with a significant higher mean cover [%]		Lichens with a significant higher constancy [%]		Total of lichen species with a mean cover > 1 %	
Type of tree	B > R	R > B	B > R	R > B	B	R
Total	14	3	16	3	10	7
Crustose	5	3	7	2	6	4
Foliose	4	0	3	1	4	2
Fruticose	3	0	3	0	0	1
Pendulous	2	0	3	0	0	0
Type of tree	DB > DR	DR > DB	DB > DR	DR > DB	DB	DR
Total	11	8	10	9	14	12
Crustose	7	4	7	6	8	8
Foliose	3	1	2	1	3	2
Fruticose	0	2	0	1	2	2
Pendulous	1	1	1	1	1	0

4.1.2 Influence of tree vitality on epiphytic lichen vegetation

Compared to living *Picea rubens*, a higher number of lichen species was found on dead spruce (40, living *P. rubens*: 35). Total mean cover did not show any difference. Dead trees had more taxa with higher mean cover, larger variation of cover, and more lichens with mean cover > 1 % than the living ones (Tab. 4-2, for detailed species list see Tab. 4-A6, Tab. 4-A3). More taxa with a higher constancy occurred on dead *Picea rubens* than on living *P. rubens* (Tab. 4-A7). 70 % (28 taxa) on dead trees never exceeded a mean cover over 1 %.

38 lichen species grew on dead *Abies balsamea* (living type: 40). Total mean cover did not differ between living and dead trees. Dead trees had more taxa with a higher mean cover, larger variation of cover, and more lichens with a mean cover > 1 % than the living ones (Tab. 4-2, for detailed species list see Tab. 4-A8, Tab. 4-A3). *Arthonia caesia* achieved only a mean cover of 9 ± 17 % on dead fir and 71 % (27 taxa) of the lichen species never exceeded a mean cover over 1%. In contrast to living and dead *Picea rubens*, total number of taxa of living and dead *Abies balsamea* did not differ in constancy (Tab. 4-2, Tab. 4-A9).

Tab. 4-2. Number of lichen taxa in a comparison of dead (DR) and living (R) *Picea rubens* as well as dead (DB) and living (B) *Abies balsamea*. n = 37.

	Lichens with a significant higher mean cover [%]		Lichens with a significant higher constancy [%]		Total of lichen species with a mean cover > 1 %	
Type of tree	DR > R	R > DR	DR > R	R > DR	DR	R
Total	15	1	19	3	12	7
Crustose	3	1	4	1	8	4
Foliose	3	0	3	2	2	2
Fruticose	7	0	8	0	2	1
Pendulous	2	0	4	0	0	0
Type of tree	DB > B	B > DB	DB > B	B > DB	DB	B
Total	5	3	7	7	14	10
Crustose	2	2	3	5	8	6
Foliose	1	1	1	2	3	4
Fruticose	2	0	3	0	2	0
Pendulous	0	0	0	0	1	0

4.1.3 Vitality of the single phorophyte

The studies in the present chapter were restricted to the bark sample trees, as in the case of the stem flow trees, not all vitality classes were found. The trees were unevenly distributed in the five vitality classes used (Ch. 3.2). It is probable that the transition from one vitality class to the next accelerates as damage proceeds and that, therefore, living trees with high damage are underrepresented.

Concerning intermediate stages between vitality classes V and I, an example of succession of cover values is illustrated in Fig. 4-1 for five selected lichen species exceeding a cover of 1 % on *Abies balsamea* and *Picea rubens*. Statistical tests could not be carried out, as only one tree of *Abies balsamea* and two trees of *Picea rubens* belonged to vitality class II.

On *Picea rubens* lichen cover increased from V to IV, except for *Lepraria jackii*. The lowest cover value for all mentioned lichens, except *Lecidea nylanderi*, was achieved in class II. *Lecidea nylanderi* had similar cover values in II than in IV. From II to I values increased again, except for *Lecidea nylanderi*, where they decreased.

On *Abies balsamea* the mentioned increase of cover from V to IV was only detected for *Imshaugia aleurites* and *Lepraria jackii*. The values of *Hypogymnia physodes* stayed similar in the two vitality classes, whereas they decreased for *Arthonia caesia* and *Lecidea nylanderi*. The lowest cover for all lichens except for *Lecidea nylanderi* was attained in class II. *Lecidea nylanderi* had the highest value in II compared to all other classes. As on *Picea rubens*, cover increased from II to I for most lichens (*Arthonia caesia*, *Hypogymnia physodes*, and *Lepraria jackii*) on *Abies balsamea*, whereas it decreased for *Imshaugia aleurites* and *Lecidea nylanderi*.

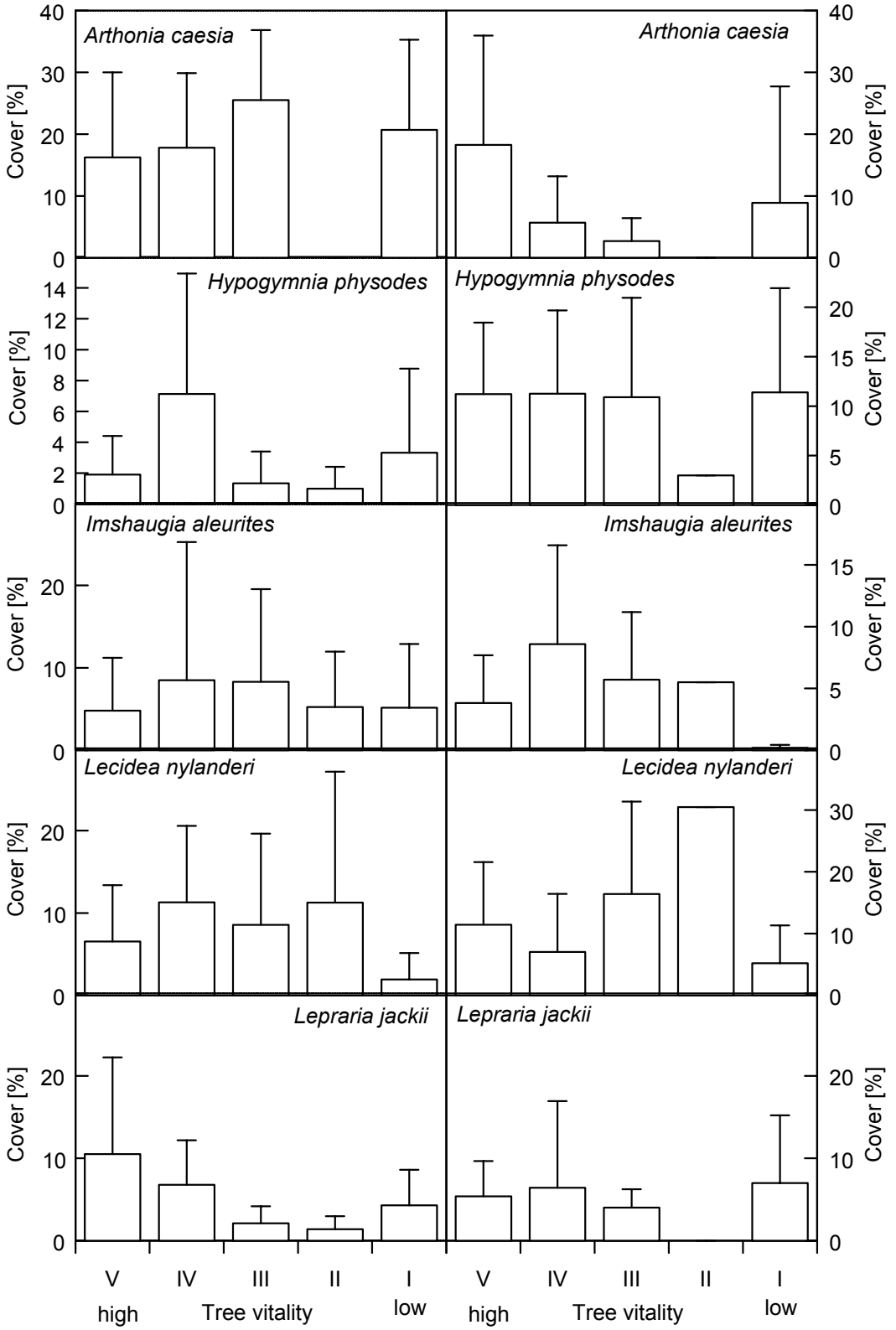

Fig. 4-1. Cover of selected lichen species depending on tree vitality. Left side: *Picea rubens*, right side: *Abies balsamea*. n: *P. rubens*: V = 14, IV = 6, III = 5, II = 2, I = 27; n: *A. balsamea*: V = 14, IV = 6, III = 5, II = 1, I = 26.

4.2 Precipitation

4.2.1 Incident precipitation

Total incident precipitation collected during the sampling periods each from June to September was 548 mm in 1999 and 483 mm in 2000. Maximum precipitation was higher in 1999 than in 2000 with 138 vs. 46 l m^{-2} $week^{-1}$ (Fig. 4-2). No significant difference occurred between total amounts of the two years (Tab. 4-3). Temporal variation during the sampling periods is shown in Fig. 4-2.

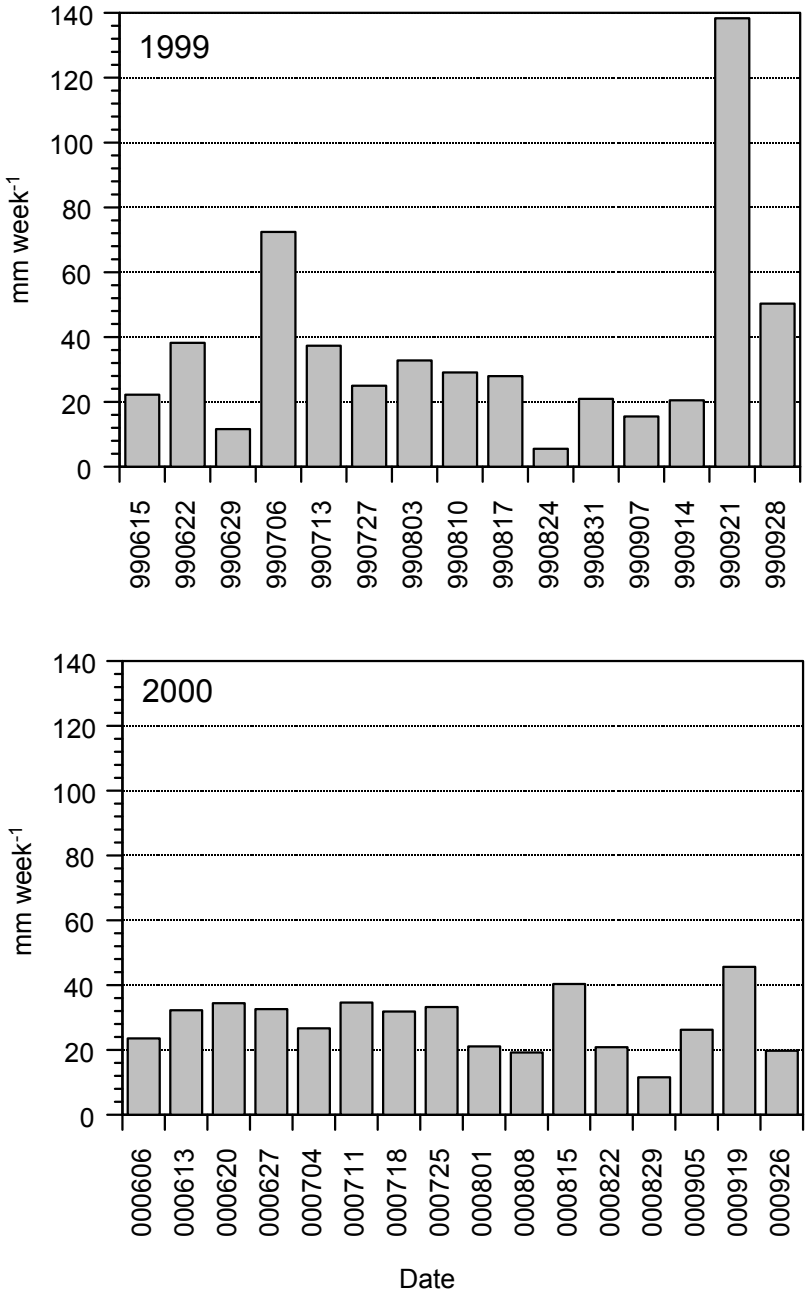

Fig. 4-2. Incident precipitation during sampling periods 1999 and 2000. n = 6.

The quantitatively most important chemical species were NH_4^+, Na, and K, followed by P, H^+, Al, NO_3^-, S, Ca, Mg, Fe, Zn, and Mn in descending order in 1999. In 2000, the order by concentration of the chemical species was NH_4^+ > P > Na > K > Al > H^+ > Ca > S > NO_3^- > Fe > Zn > Mg > Mn. The chemical composition of the incident precipitation differed between 1999 and 2000 for NO_3^-, P, K, Na, Ca, Fe, Mn, and Zn (Tab. 4-3). NO_3^-, K, and Na occurred in higher concentrations in 1999 than in 2000, whereas the same was true for P, Ca, Fe, Mn, and Zn in 2000. Ranges of element concentrations and medians in incident precipitation are given in Tab. 4-A10 in the appendix.

Tab. 4-3. Element content and amounts of incident precipitation.

	1999	2000	1999/2000	
NH_4^+ [µmol l^{-1}]	62.1 ± 46.5	67.0 ± 35.7	64.7 ± 41.2	
NO_3^- [µmol l^{-1}]	4.01 ± 4.20	2.49 ± 2.74	3.22 ± 3.59	*
P [µmol l^{-1}]	4.88 ± 2.29	17.9 ± 6.30	11.6 ± 8.09	***
S [µmol l^{-1}]	2.51 ± 1.53	2.11 ± 1.25	2.30 ± 1.40	
K [µmol l^{-1}]	16.5 ± 10.3	11.8 ± 16.5	14.0 ± 14.0	***
Na [µmol l^{-1}]	18.8 ± 4.80	16.7 ± 2.8	17.7 ± 4.01	***
Ca [µmol l^{-1}]	3.16 ± 3.20	4.23 ± 1.20	3.72 ± 2.44	***
Mg [µmol l^{-1}]	0.69 ± 1.17	0.39 ± 0.40	0.54 ± 0.87	
Fe [µmol l^{-1}]	0.25 ± 0.22	0.64 ± 0.24	0.45 ± 0.30	***
Mn [µmol l^{-1}]	0.10 ± 0.19	0.18 ± 0.10	0.14 ± 0.15	***
Al [µmol l^{-1}]	4.10 ± 1.21	4.33 ± 1.74	4.22 ± 1.51	
Zn [µmol l^{-1}]	0.13 ± 0.08	0.45 ± 0.16	0.30 ± 0.21	***
pH	4.41 ± 0.21	4.39 ± 0.17	4.40 ± 0.18	
Conductivity [µS cm^{-1}]	20.8 ± 10.6	21.1 ± 8.7	21.0 ± 9.63	
Precipitation [l m^{-2} $week^{-1}$]	36.5 ± 31.9	28.4 ± 8.9	32.3 ± 23.3	

Arithmetic mean ± standard deviation. Statistics: U-test; significant differences are between the years. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. n = 6. Measuring periods: June – September; 15 weeks in 1999, 16 weeks in 2000; weekly measurements.

Many strong correlations occurred between element concentrations in incident precipitation in 1999, fewer in 2000 (Tab. 4-A11 – 4-A12). When $r^2 \geq 40$ % was taken as a borderline for notable correlation, NO_3^-, for instance, was correlated in 1999 with Na, Fe, Zn, but not in 2000; S, Ca, Mg, pH, and conductivity were correlated with NO_3^- in both years. NH_4^+, as another example, correlated with Fe in 1999, but not in 2000. Elements such as P, K, Na, Ca, Fe, Zn, and Cu did not correlate with any other element in 2000, but in 1999 (Tab. 4-A11 – 4-A12). Complete Spearman correlation matrices calculated separately for the two sampling periods and for the mean of all data are given in Tab. 4-A11 – 4-A13 in the appendix.

4.2.2 Stem flow

4.2.2.1 Influence of tree species on quantity and chemical composition of the stem flow

The amount of stem flow per tree per week did not differ between living *Abies balsamea* and living *Picea rubens*, but was higher on dead *P. rubens* than on dead *A. balsamea* (Tab. 4-4).

Differences in the concentration of chemical species between living fir and living spruce occurred for P, S, K, Na, Mn, Al, Cu, H^+, and NO_3^-. Except for NO_3^- and H^+, all these elements were less concentrated in stem flow of living *Picea rubens* than of living *Abies balsamea*. In the case of P, S, Na, and H^+, concentrations differed significantly between living spruce and fir in 1999, but not in 2000. Cu occurred in higher concentrations on living fir only in 2000. In most cases element concentrations in stem flow of living fir varied more than that of living spruce. Comparing ranges of the element contents, in 11 out of 17 cases *Abies balsamea* showed a higher variability than *Picea rubens* (Tab. 4-A14 – 4-A17 in the appendix). K was the most common chemical species in the stem flow of living *Abies balsamea* (Fig. 4-3), followed by H^+. On living *Picea rubens*, K was subordinate in comparison to H^+. Among the elements, which were only found in concentrations below 10 µmol l^{-1}, NO_3^- had a significant lower mean content in the stem flow of living *Abies balsamea* than in the stem flow of living *Picea rubens*. A complete table of all elements and the amounts of stem flow is given in Tab. 4-4.

Stem flow of dead *Picea rubens* contained higher concentrations of the chemical species NO_3^-, Ca, Mn, and Al than that of dead *Abies balsamea*. NO_3^- showed these differences in 1999, as did Ca and Mn in 2000 (Tab. 4-4). The pH was lower in the stem flow of dead *Picea rubens* than that of dead *Abies balsamea*. The range of the element contents was wider in 10 out of 17 cases for *Picea rubens* than for *Abies balsamea* (Tab. 4-A15 and 4-A17). The most common chemical species in the stem flow of the two tree species was K (Fig. 4-3). The difference of NO_3^- in the stem flow between the dead tree species was significant (dead *Abies balsamea* < dead *Picea rubens*), but not as obvious as between the living types of trees.

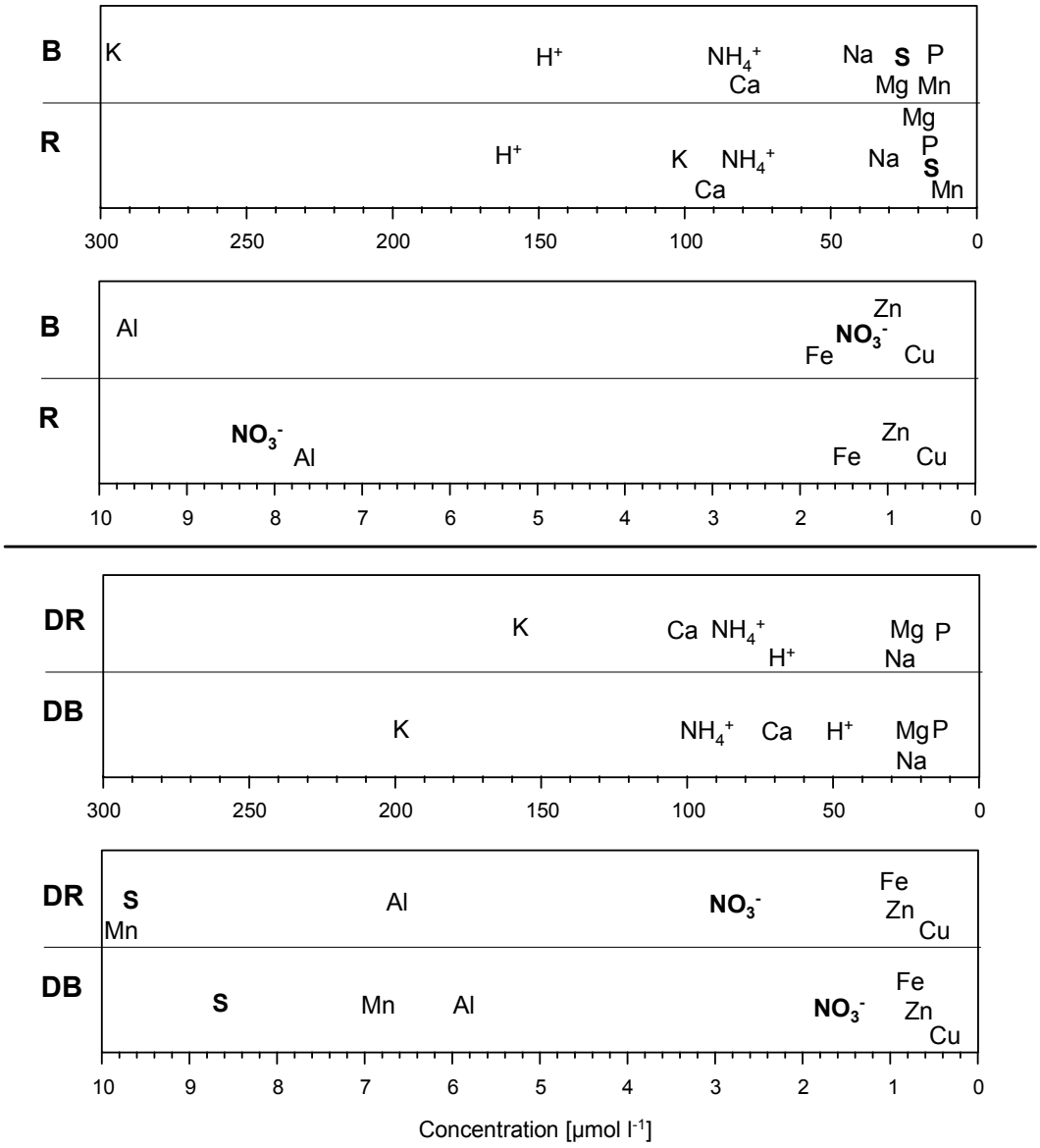

Fig. 4-3. Mean concentration [µmol l^{-1}] of the chemical species investigated in the stem flow of living *Abies balsamea* (B) and living *Picea rubens* (R) as well as dead *P. rubens* (DR) and dead *A. balsamea* (DB). Data were calculated from means of every sample tree over the entire period of sampling. Bold-faced type: Elements of which there is experimental evidence that the ambient levels affect lichen growth.

Tab. 4-4. Element content of stem flow of living (R) and dead (DR) *Picea rubens* as well as living (B) and dead (DB) *Abies balsamea*.

	Year	R		DR		B		DB	
NH_4^+ [µmol l^{-1}]	1999	103 ± 44.6	a	101 ± 39.5	a	111 ± 35.3	a	135 ± 89.5	a
	2000	60.5 ± 12.2	a	60.3 ± 13.9	a	64.3 ± 11.1	a	62.4 ± 10.2	a
	99/00	81.5 ± 27.2	a	80.6 ± 20.7	a	84.2 ± 17.0	a	98.8 ± 44.2	a
NO_3^- [µmol l^{-1}]	1999	15.8 ± 13.3	a	5.40 ± 2.06	b	2.26 ± 1.29	c	3.24 ± 1.34	c
	2000	0.76 ± 1.15	a	0.24 ± 0.22	ab	0.15 ± 0.17	b	0.21 ± 0.16	ab
	99/00	8.27 ± 7.13	a	2.82 ± 1.04	b	1.16 ± 0.69	c	1.73 ± 0.71	c
P [µmol l^{-1}]	1999	6.04 ± 1.11	a	8.42 ± 4.24	ab	9.35 ± 2.82	b	12.0 ± 7.31	b
	2000	18.9 ± 0.92	a	19.7 ± 1.45	ab	20.3 ± 2.50	ab	20.1 ± 1.46	b
	99/00	12.5 ± 0.73	a	14.1 ± 2.49	ab	14.8 ± 2.45	b	16.0 ± 4.00	b
S [µmol l^{-1}]	1999	18.0 ± 6.92	a	11.6 ± 2.49	b	28.6 ± 7.58	c	11.4 ± 2.50	b
	2000	13.3 ± 2.75	a	7.70 ± 2.57	b	16.6 ± 4.37	a	5.93 ± 2.94	b
	99/00	15.6 ± 4.50	a	9.64 ± 2.16	b	22.4 ± 5.61	c	8.65 ± 2.46	b
K [µmol l^{-1}]	1999	116 ± 38.7	a	178 ± 146	ab	357 ± 124	c	240 ± 116	bc
	2000	88.8 ± 25.0	a	131 ± 82.6	a	237 ± 75.5	b	151 ± 97.5	ab
	99/00	103 ± 30.1	a	155 ± 110	ac	295 ± 101	b	195 ± 98.9	c
Na [µmol l^{-1}]	1999	38.4 ± 5.40	a	30.8 ± 3.19	b	51.1 ± 9.42	c	30.5 ± 6.26	bd
	2000	28.0 ± 2.47	a	21.0 ± 1.66	b	30.3 ± 4.47	a	20.2 ± 2.31	b
	99/00	33.2 ± 3.80	a	25.9 ± 2.01	b	40.1 ± 6.56	c	25.3 ± 4.03	b
Ca [µmol l^{-1}]	1999	108 ± 42.4	a	106 ± 42.5	a	98.3 ± 22.9	a	88.9 ± 32.7	a
	2000	75.9 ± 21.4	a	99.2 ± 64.3	a	63.9 ± 19.3	ab	53.0 ± 34.9	b
	99/00	91.9 ± 27.2	a	103 ± 50.9	a	79.9 ± 18.0	a	71.0 ± 29.4	a
Mg [µmol l^{-1}]	1999	27.2 ± 12.3	a	25.2 ± 8.54	a	33.4 ± 10.6	a	31.7 ± 10.7	a
	2000	17.7 ± 5.72	a	22.0 ± 11.2	a	19.7 ± 6.55	a	17.9 ± 11.1	a
	99/00	22.4 ± 8.06	a	23.6 ± 8.88	a	26.0 ± 7.43	a	24.8 ± 9.1	a

(Cont.)

(Cont. Tab. 4-4)

	Year	R		DR		B		DB	
Fe [µmol l^{-1}]	1999	1.42 ± 0.43	a	0.71 ± 0.17	b	1.72 ± 0.43	a	0.65 ± 0.15	b
	2000	1.68 ± 0.21	a	1.06 ± 0.23	b	1.76 ± 0.42	a	0.91 ± 0.17	b
	99/00	1.55 ± 0.29	a	0.88 ± 0.19	b	1.74 ± 0.42	a	0.78 ± 0.15	b
Mn [µmol l^{-1}]	1999	13.6 ± 5.98	abc	9.99 ± 3.43	ac	18.3 ± 7.82	b	9.49 ± 7.29	c
	2000	10.2 ± 4.18	a	9.63 ± 5.99	a	12.5 ± 8.66	a	4.28 ± 4.64	b
	99/00	11.9 ± 4.38	a	9.81 ± 4.28	ab	15.5 ± 7.71	a	6.89 ± 5.72	b
Al [µmol l^{-1}]	1999	8.16 ± 1.16	a	6.79 ± 0.53	b	10.6 ± 1.48	c	6.16 ± 0.46	d
	2000	7.05 ± 0.51	a	6.45 ± 0.68	a	8.83 ± 1.24	b	5.62 ± 0.61	c
	99/00	7.61 ± 0.70	a	6.62 ± 0.54	b	9.73 ± 1.32	c	5.89 ± 0.51	d
Zn [µmol l^{-1}]	1999	0.92 ± 0.68	a	0.64 ± 0.21	a	0.78 ± 0.21	a	0.62 ± 0.19	a
	2000	0.91 ± 0.29	a	1.01 ± 0.43	a	0.79 ± 0.21	a	0.72 ± 0.21	a
	99/00	0.92 ± 0.48	a	0.83 ± 0.30	a	0.77 ± 0.20	a	0.67 ± 0.17	a
Cu [µmol l^{-1}]	1999	0.37 ± 0.02	abc	0.36 ± 0.04	ac	0.43 ± 0.10	b	0.35 ± 0.03	c
	2000	0.68 ± 0.03	a	0.72 ± 0.05	ac	0.81 ± 0.03	b	0.72 ± 0.04	c
	99/00	0.52 ± 0.02	a	0.54 ± 0.03	a	0.62 ± 0.06	b	0.54 ± 0.02	a
pH	1999	3.74 ± 0.10	a	4.17 ± 0.11	b	3.83 ± 0.08	c	4.35 ± 0.14	d
	2000	3.83 ± 0.10	a	4.18 ± 0.13	b	3.85 ± 0.12	a	4.24 ± 0.15	c
	99/00	3.79 ± 0.10	a	4.18 ± 0.12	b	3.84 ± 0.10	c	4.30 ± 0.15	d
Conductivity [µS cm^{-1}]	1999	112 ± 32.6	a	74.0 ± 14.8	b	139 ± 30.6	a	72.3 ± 12.1	b
	2000	90.2 ± 14.9	a	63.7 ± 17.8	b	107 ± 29.2	a	53.8 ± 12.4	b
	99/00	101 ± 20.1	a	68.9 ± 13.7	b	123 ± 29.0	a	63.0 ± 11.1	b
Stem flow	1999	1.40 ± 0.70	ab	1.10 ± 0.40	a	1.10 ± 0.50	ab	0.80 ± 0.50	b
[l $tree^{-1}$ $week^{-1}$]	2000	1.70 ± 1.10	a	1.30 ± 0.60	a	1.20 ± 1.00	ab	0.60 ± 0.50	b
	99/00	1.50 ± 0.90	a	1.20 ± 0.50	a	1.20 ± 0.70	ab	0.70 ± 0.50	b

Arithmetic mean ± standard deviation. Statistic: U-Test, $p \leq 0.05$. Measuring period 1999: June – September (15 weeks); measuring period 2000: June – September (16 weeks); weekly sampling. n = 10, tree type B in 2000: n = 9. Data are calculated from means of every sample tree over the entire measuring period.

4.2.2.2 Influence of tree vitality on quantity and chemical composition of the stem flow

The amount of mean stem flow per tree per week did not differ between living and dead *Picea rubens* nor between living and dead *Abies balsamea* (Tab. 4-4).

In comparison to the dead trees, live trees of both species had higher concentrations in the stem flow of the chemical species S, Na, Fe, and Al as well as a higher conductivity. This was also true for Mn and Cu in the stem flow of *Abies balsamea*. Higher concentrations of NO_3^- occurred in 1999 in the stem flow of living *Picea rubens*. The pH was lower in the stem flow of the living trees of each species than of the dead ones. With living *Picea rubens* the data varied more than with dead *P. rubens*. In 11 out of 17 cases the range of the element contents was wider for living spruce (Tab. 4-A16 – Tab. 4-A17). The same was true for the comparison of living and dead fir (Tab. 4-A14 – Tab. 4-A15). In the comparison of living and dead *Picea rubens* the most common chemical species was H^+ for the living type of tree and K for the dead one. K was also the most common species for both types of *Abies balsamea* (Fig. 4-4).

A two-way analysis of variance (ANOVA) of the independent variables 'tree species' and 'tree vitality' revealed that tree vitality had the highest impact on most of the chemical parameters (Tab. 4-A18 - Tab. 4-A19). For 'tree vitality', r^2 was more than 46 % for S, Na, Fe, Al, pH, and conductivity in 1999 as well as in 2000. Furthermore, there was a weak influence by this variable on Mn and Cu content of stem flow. Concerning 'tree species', r^2 was highest for K (r^2 = 28 %) and NO_3^- (r^2 = 21 %) in 1999 as well as for K (r^2 = 21 %) and Cu (r^2 = 29 %) in 2000.

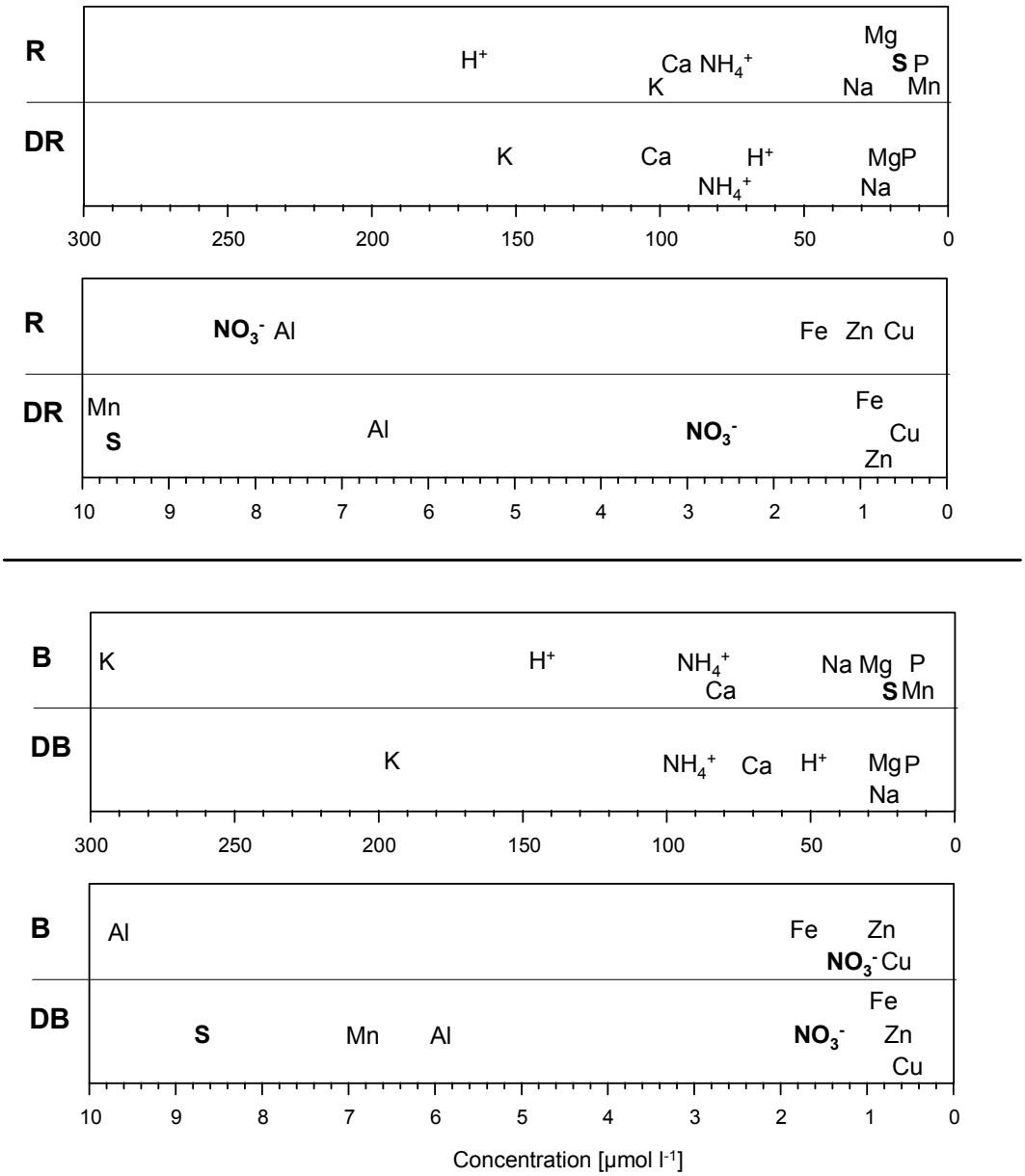

Fig. 4-4. Mean concentration [µmol l^{-1}] of the chemical species investigated in the stem flow of living (R) and dead (DR) *Picea rubens* and living (B) and dead (DB) *Abies balsamea*. Data were calculated from means of every sample tree over the entire period of sampling. Bold-faced type: Elements for which there is experimental evidence that the ambient levels affect lichen growth.

4.2.2.3 Seasonal variability of elements in the stem flow

Presentation of the seasonal variability of the elements is restricted to NO_3^-, Ca, S, and Mn, as these elements correlated with the cover of epiphytic lichen species (Fig. 4-5 – Fig. 4-8).

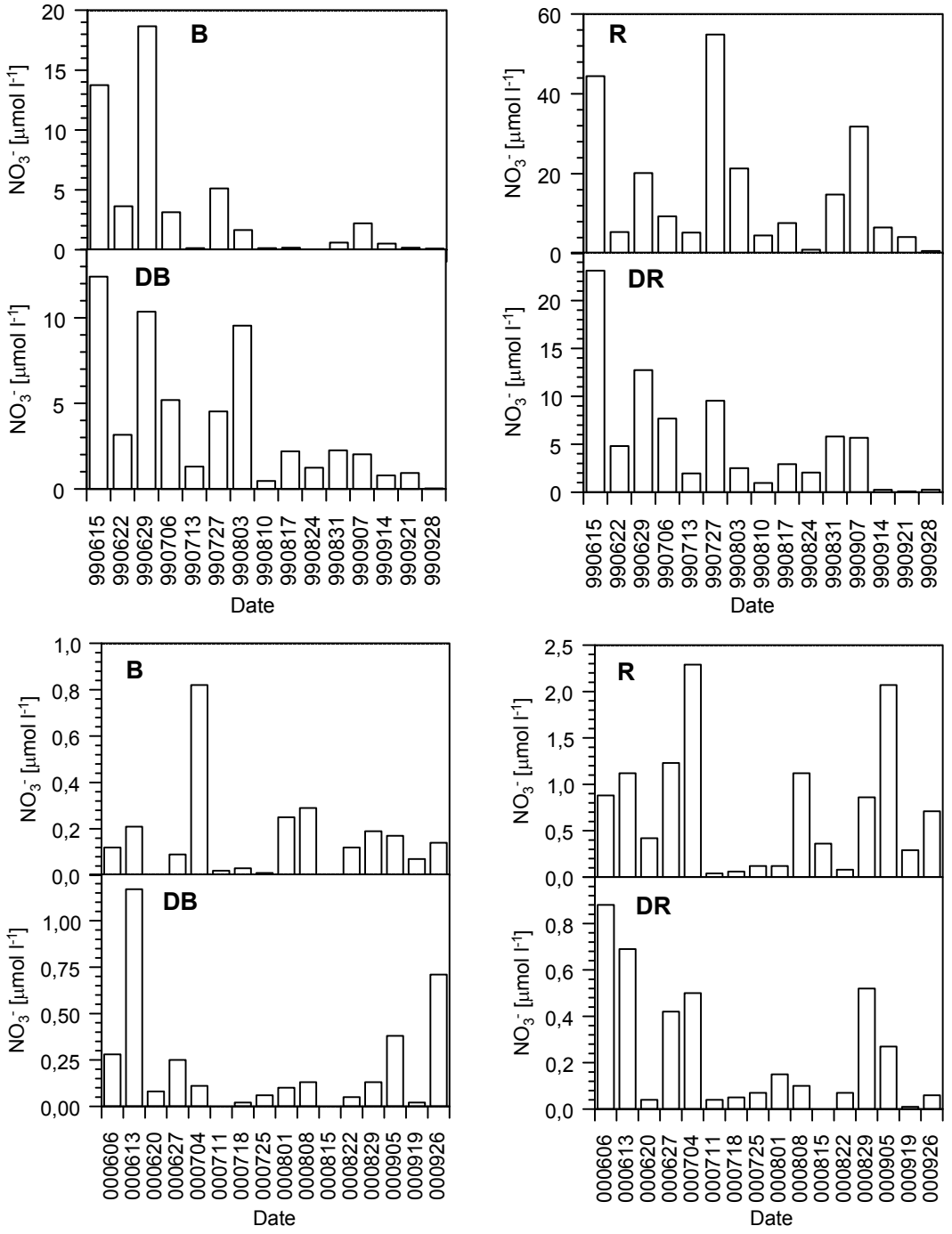

Fig. 4-5. Seasonal variability of NO_3^- in stem flow. Data were calculated from means of every sample tree over the entire period of sampling. Above: 1999, below: 2000. n = 10 for each type of tree and each sampling date.

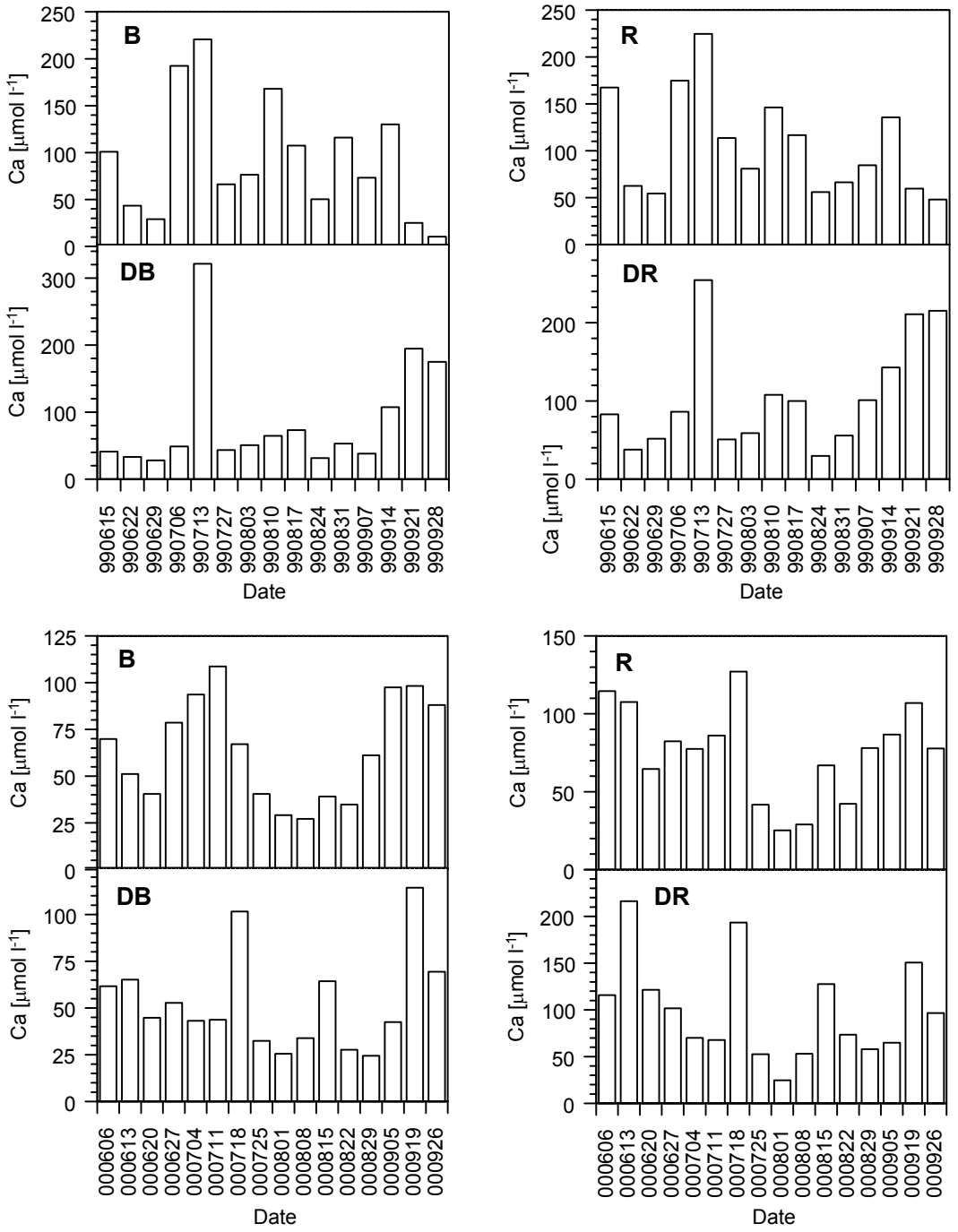

Fig. 4-6. Seasonal variability of Ca in stem flow. Data were calculated from means of every sample tree over the entire period of sampling. Above: 1999, below: 2000. n = 10 for each type of tree and each sampling date.

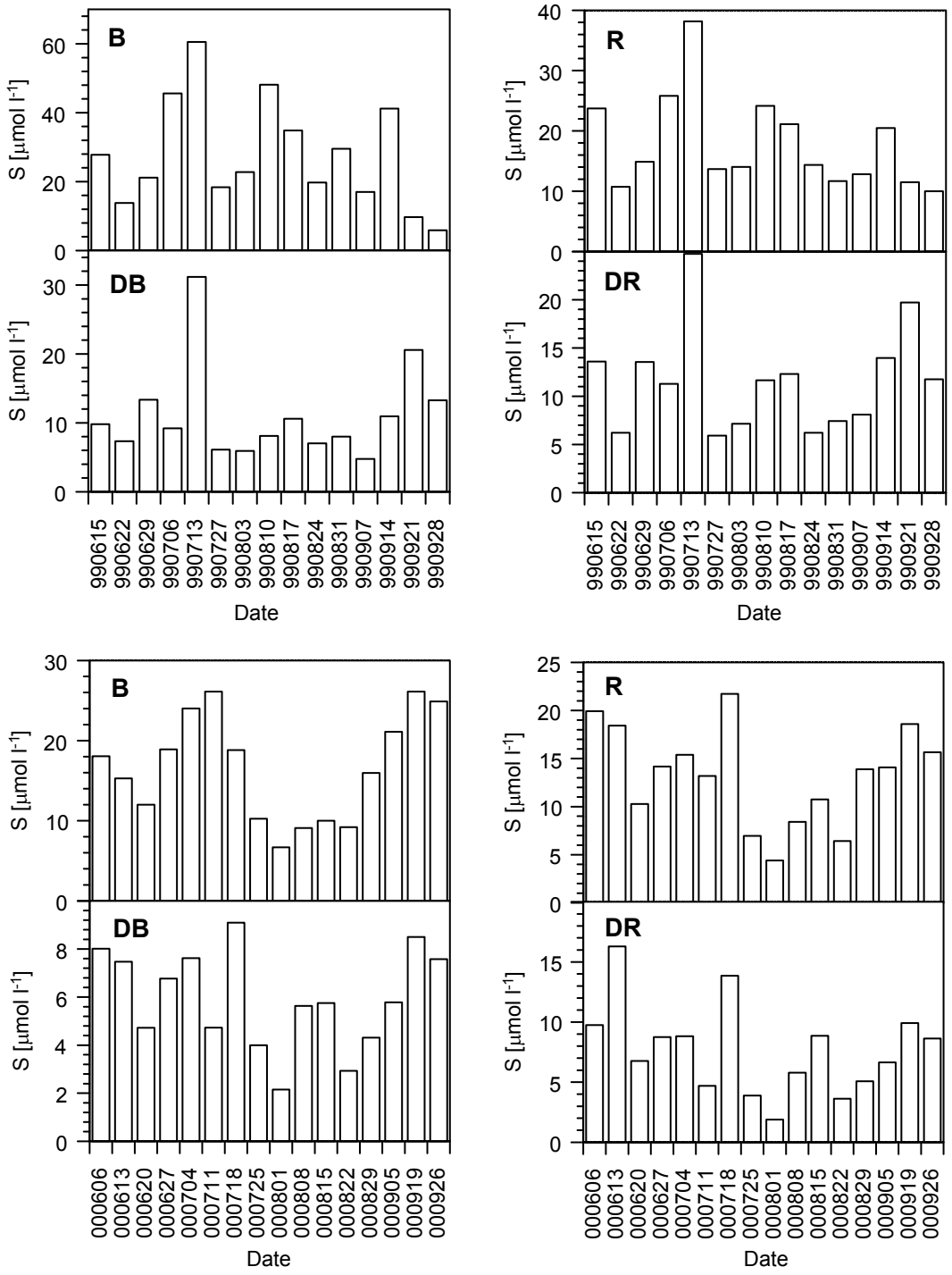

Fig. 4-7. Seasonal variability of S in stem flow. Data were calculated from means of every sample tree over the entire period of sampling. Above: 1999, below: 2000. n = 10 for each type of tree and each sampling date.

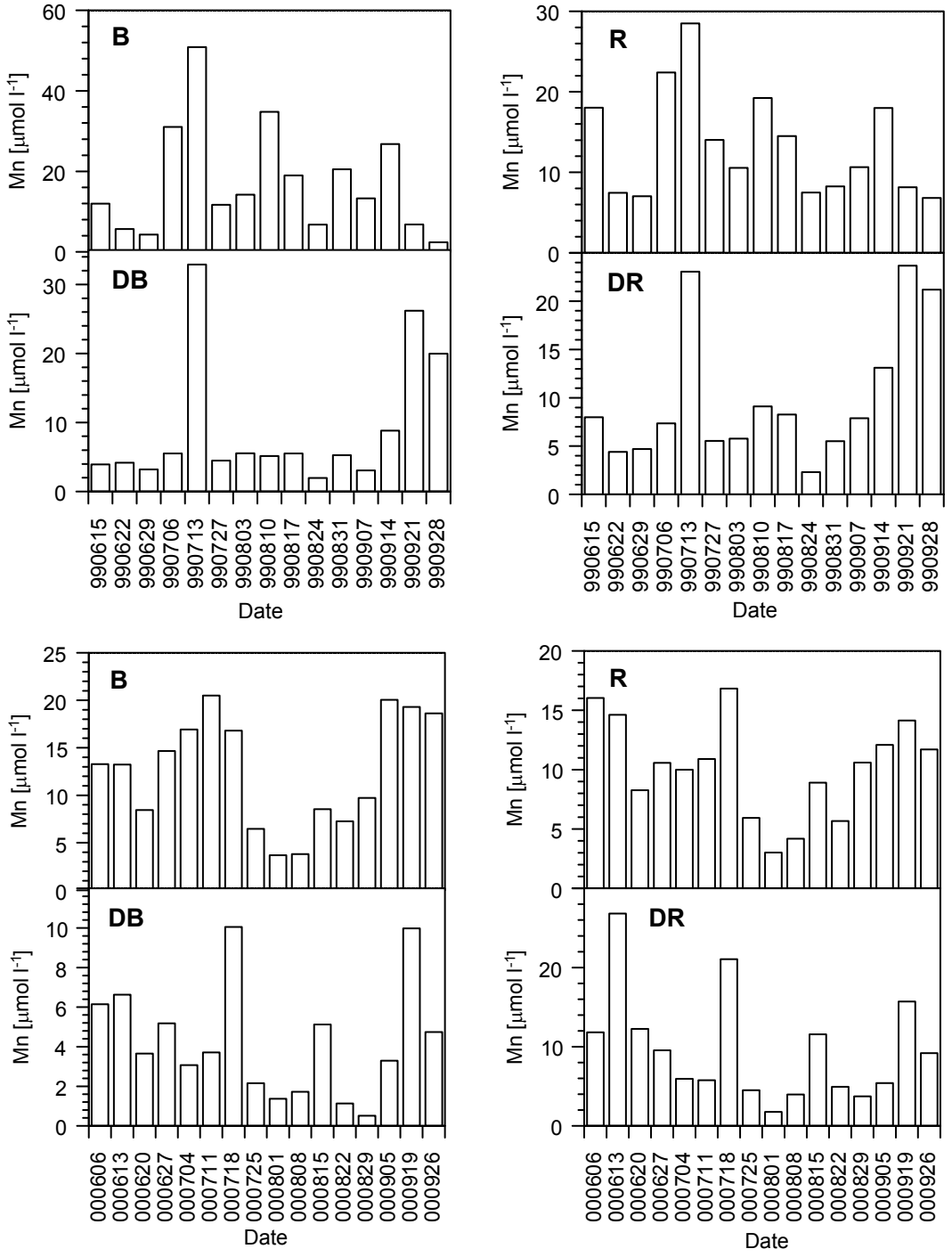

Fig. 4-8. Seasonal variability of Mn in stem flow. Data were calculated from means of every sample tree over the entire period of sampling. Above: 1999, below: 2000. n = 10 for each type of tree and each sampling date.

4.2.3 Correlations between parameters

Correlation analyses were carried out for 1999, 2000, and for the mean of 1999/2000, for each of the tree species, divided into living and dead types. Spearman correlation matrices are given in Tab. 4-A21 – 4-A32 in the appendix. S, K, Na, Ca, Mg, Fe, Mn, and Al formed a group of elements in 1999 in the stem flow of living *Picea rubens* which correlated with one another with $r^2 \geq 50$ %. This tendency applied also to dead trees of spruce and fir, as well as for living *Abies balsamea* for 1999, 2000, and 1999/2000. NH_4^+, NO_3^-, and P correlated with fewer elements. There was only one rather weak correlation between pH and conductivity in the stem flow of living *Picea rubens* in 1999 and in 1999/2000, as there was between volume and NH_4^+ in 2000 of dead *P. rubens*.

4.2.4 Correlations with incident precipitation

Out of 16 parameters measured in stem flow of the different types of trees in 1999 and 2000, concentrations of NH_4^+, NO_3^-, P, S, Na, Mg, Fe, Zn, and Cu as well as pH, conductivity, and water volume were correlated with the corresponding variables in incident precipitation (Tab. 4-A33). Fig. 4-9 shows as an example the correlation between amounts of stem flow and incident precipitation in 2000.

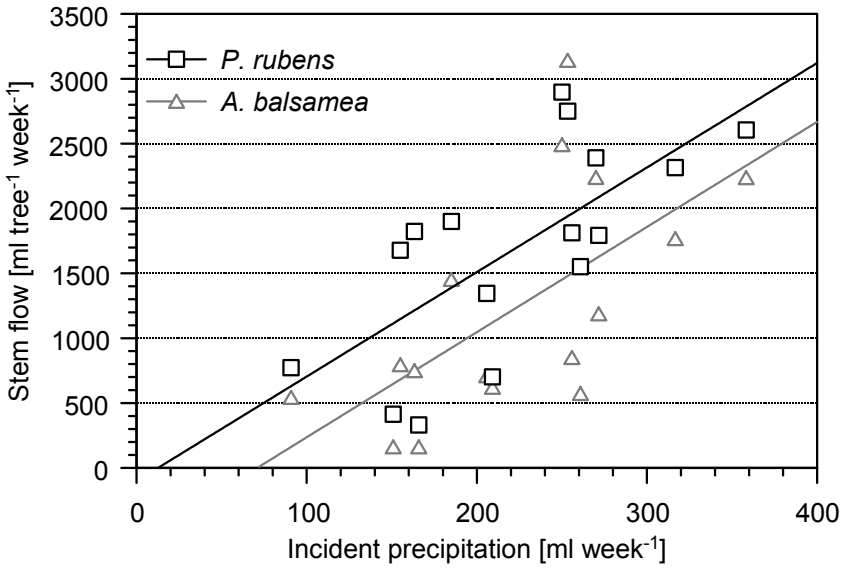

Fig. 4-9. Correlation between stem flow and incident precipitation at living *Abies balsamea* and *Picea rubens*. Dots represent weekly mean values of 10 sample trees per species, and 6 rain samplers. *P. rubens*: r = 0.69, $p \leq 0.01$; *A. balsamea*: r = 0.63, $p \leq 0.01$.

4.3 Bark

4.3.1 Element content of bark

4.3.1.1 Influence of tree species on chemical composition of the bark

Differences in the mean content in the bark between living *Abies balsamea* and *Picea rubens* were detected for N, C, K, Mg, Fe, Mn, Zn, and Cu (Tab. 4-5). Except for Fe and H^+, all elements were more concentrated in the bark of *Abies balsamea* than of *Picea rubens*. Most parameters had a larger range on living *Abies balsamea* than on living *Picea rubens*, i.e. N, K, Mg, Fe, Mn, Cu, and H^+ (Tab. 4-A34, 4-A36). C, Ca, Zn, Pb, and conductivity had wider ranges on *Picea rubens*. The coefficients of variation did not considerably differ between living spruce and fir. Coefficients of variation for Mg, Fe, Mn, Pb, and H^+ were higher on *Abies balsamea*, whereas N, C, K, Ca, Zn, Cu, and conductivity had a higher coefficient of variation on *Picea rubens*.

In a comparison between dead spruce and dead fir, mean content of N, C, K, Mg, Mn, and Cu was higher in *Abies balsamea* than in *Picea rubens* (Tab. 4-5). The former species also had a wider range for all parameters investigated (Tab. 4-A35, 4-A37). Additionally, most parameters showed a higher coefficient of variation except for Ca, Mg, and Pb, which were higher on dead *Picea rubens*.

4.3.1.2 Influence of tree vitality on chemical composition of the bark

Mean bark content of C, K, Ca, Mg, Mn, Zn, and Cu and mean H^+ differed between living and dead *Picea rubens*, whereby bark of living spruce contained more K, Ca, Mg, Mn, Zn, and H^+ (Tab. 4-5). Only C and Cu were more concentrated in dead *Picea rubens*. Most of the parameters showed a wider range (except for Mg) and a higher coefficient of variation (except for Mg and Pb) on living *Picea rubens* (Tab. 4-A34 - 4-A35).

Concentrations of N, C, K, Ca, and Mn as well as conductivity differed in their mean content between living and dead *Abies balsamea* (Tab. 4-5). Concentrations of C, K, Mn, and conductivity were higher in the bark of living fir, whereas N and Ca were higher in the bark of dead fir. On *Abies balsamea* most parameters had a wider range and a higher coefficient of variation on dead trees than on living ones (Tab. 4-A36 - 4-A37). As for the range, N, K, Fe, and Mn were higher on living *Abies balsamea* and Fe, Zn, and Pb had a higher coefficient of variation.

In a two-way analysis of variance (ANOVA) of the independent variables ‘tree species’ and ‘tree vitality’, less of the variance of the chemical parameters could be explained by the model than in the case of stem flow (Tab. 4-A38). N, K, Cu, and pH were influenced most by the variable ‘tree species’ with $r^2 \geq 48$ %. Moreover, weak influences of the variable occurred on C, Mg, and Mn content of the substrate.

Tab. 4-5. Bark content in living (R) and dead (DR) *Picea rubens* as well as living (B) and dead (DB) *Abies balsamea*.

	R		DR		B		DB	
N [µmol g^{-1}]	233 ± 55.5	a	217 ± 30.5	a	363 ± 60.3	b	461 ± 80.0	c
C [mmol g^{-1}]	41.0 ± 1.93	a	40.2 ± 1.04	b	44.4 ± 1.65	c	42.6 ± 1.74	d
K [µmol g^{-1}]	6.83 ± 7.76	a	10.3 ± 4.88	b	38.9 ± 18.0	c	26.6 ± 13.4	d
Ca [µmol g^{-1}]	158 ± 48.5	ac	190 ± 56.2	bd	134 ± 29.2	a	183 ± 50.5	cd
Mg [µmol g^{-1}]	4.32 ± 1.28	a	8.27 ± 4.41	b	9.24 ± 2.90	bc	14.3 ± 6.94	c
Fe [µmol g^{-1}]	1.47 ± 0.64	a	1.36 ± 0.51	ac	1.12 ± 0.76	b	1.19 ± 0.52	bc
Mn [µmol g^{-1}]	6.91 ± 2.83	a	8.41 ± 2.50	b	29.3 ± 21.5	c	19.0 ± 14.3	d
Zn [µmol g^{-1}]	0.93 ± 0.40	a	1.11 ± 0.32	b	1.16 ± 0.44	b	1.31 ± 0.47	b
Pb [µmol g^{-1}]	0.02 ± 0.04	a	0.01 ± 0.02	a	0.00 ± 0.01	a	0.01 ± 0.03	a
Cu [µmol g^{-1}]	0.06 ± 0.02	a	0.05± 0.01	b	0.12 ± 0.02	c	0.11 ± 0.03	c
pH (H_2O)	3.44 ± 0.19	a	3.58 ± 0.16	b	3.97 ± 0.24	c	4.11 ± 0.26	c
pH (KCl)	3.06 ± 0.15	a	3.17 ± 0.15	b	3.49 ± 0.23	c	3.58 ± 0.36	c
Conductivity [µS cm^{-1}]	174 ± 49.8	ab	176 ± 43.2	ab	189 ± 39.6	a	159 ± 47.1	b

Arithmetic mean ± standard deviation. Statistics: U-Test; $p \leq 0.05$. n = 27.

4.3.2 Comparison of different extractants

4.3.2.1 Effects of extraction media on extracted element content

Mean content in the extractions with H_2O of K, Mg, Mn, Zn, and Cu was higher in the bark of *Abies balsamea* than of *Picea rubens* (Tab. 4-6). A higher range of Mg, Ca, and Mn was also achieved in *Abies balsamea* (Tab. 4-A39 - Tab. 4-A40). When mean concentrations of the water eluates were related to the total content of the corresponding element in the bark, Mg was extracted to a higher extent from *Abies balsamea* than from *Picea rubens*, whereas more K was extracted from *P. rubens* (Tab. 4-A41).

EDTA extractions showed higher mean contents of K, Mg, Mn, Zn, and Cu in the bark samples of *Abies balsamea* than of *Picea rubens* (Tab. 4-6). Mg, Ca, Zn, and Mn also had a higher range in *Abies balsamea* (Tab. 4-A39 - Tab. 4-A40). Mg, Fe, Mn, and Zn were more effectively extracted by EDTA from fir, whereas K was extracted to a higher extend from spruce (Tab. 4-A41).

Extractions with $SrCl_2$ gave significant differences in the mean content of K, Mg, Fe, and Mn, whereby, except for Fe, concentrations in *Abies balsamea* were higher than in *Picea rubens* (Tab. 4-6). A higher range was reached in fir for Mg, Ca, Zn, and Mn (Tab. 4-A39 - Tab. 4-A40). K, Fe, Mn, Zn, and Cu were more effectively extracted from spruce bark, whereas Mg was extracted to a higher extent from *Abies balsamea* (Tab. 4-A41).

Abies balsamea had higher mean values in total bark content of K, Mg, Mn, and Cu (Tab. 4-6). K, Mg, Ca, Zn, and Mn showed also a wider range in fir than in spruce, whereas the range of Fe was bigger in the latter tree species (Tab. 4-A439 - Tab. 4-A40). For 95 % confidence limits of the mean of element content for all extractants consult Tab. 4-A42 and Tab. 4-A43 in the appendix.

Tab. 4-6. Mean content of elements [mmol kg-1 DW] of extractions with deionised H2O, EDTA, and SrCl2 as well as of total bark content.

	A. balsamea	*P. rubens*	
H_2O eluate:			
K	15.4 ± 8.32	5.42 ± 5.99	***
Ca	3.41 ± 2.07	3.87 ± 1.91	
Mg	1.68 ± 0.77	0.71 ± 0.42	***
Fe	0.02 ± 0.01	0.02 ± 0.01	
Mn	2.10 ± 2.00	0.46 ± 0.23	***
Zn	0.08 ± 0.05	0.04 ± 0.03	*
Cu	0.02 ± 0.01	0.01 ± 0.00	*
EDTA extract:			
K	23.2 ± 12.1	8.49 ± 9.59	***
Ca	35.5 ± 22.9	25.7 ± 11.9	
Mg	5.35 ± 2.17	2.55 ± 1.45	***
Fe	0.53 ± 0.23	0.45 ± 0.28	
Mn	22.7 ± 14.1	5.04 ± 2.25	***
Zn	1.21 ± 0.43	1.14 ± 1.40	*
Cu	0.07 ± 0.02	0.05 ± 0.02	***
$SrCl_2$ extract:			
K	25.9 ± 12.5	10.1 ± 12.0	***
Ca	52.5 ± 24.6	50.3 ± 15.1	
Mg	10.7 ± 5.90	4.27 ± 2.55	***
Fe	0.02 ± 0.01	0.03 ± 0.01	**
Mn	13.7 ± 9.40	4.24 ± 1.70	***
Zn	0.43 ± 0.11	0.59 ± 0.76	
Cu	0.02 ± 0.01	0.02 ± 0.00	
Total bark content:			
K	36.5 ± 25.0	15.2 ± 18.4	***
Ca	133 ± 47.2	144 ± 69.0	
Mg	16.7 ± 9.12	8.38 ± 3.46	***
Fe	1.20 ± 0.45	1.25 ± 0.74	
Mn	22.7 ± 14.4	6.20 ± 2.62	***
Zn	1.26 ± 0.32	1.35 ± 1.56	
Cu	0.26 ± 0.08	0.19 ± 0.06	**

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance:
* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. n = 20. Total bark content extracted with HNO_3.

4.3.3 Microdistribution of chemical elements in the bark of *Abies balsamea* and *Picea rubens*

Mn is known to reduce soredia growth of *Hypogymnia physodes* at 3 mM and structural deformation of both lichen symbionts of *H. physodes* was detected at a concentration of 7 mM Mn (HAUCK et al. 2002, Paul unpubl.). According to the higher lichen growth on *Abies balsamea* than on *Picea rubens* (Tab. 4-1) in combination with the high Mn content in the bark of the former species (Tab. 4-5), investigations about the microdistribution of chemical elements in the bark of the two tree species were carried out. Bark of *Abies balsamea* consists of the same types of cells as bark of *Picea rubens*, namely cortex parenchyma, one or more layers of spongy cork cells and phlobaphene cork cells as well as sclerotic phelloids (PARAMESWARAN et al. 1976). In between, fibre cells can be found (Fig. 4-10).

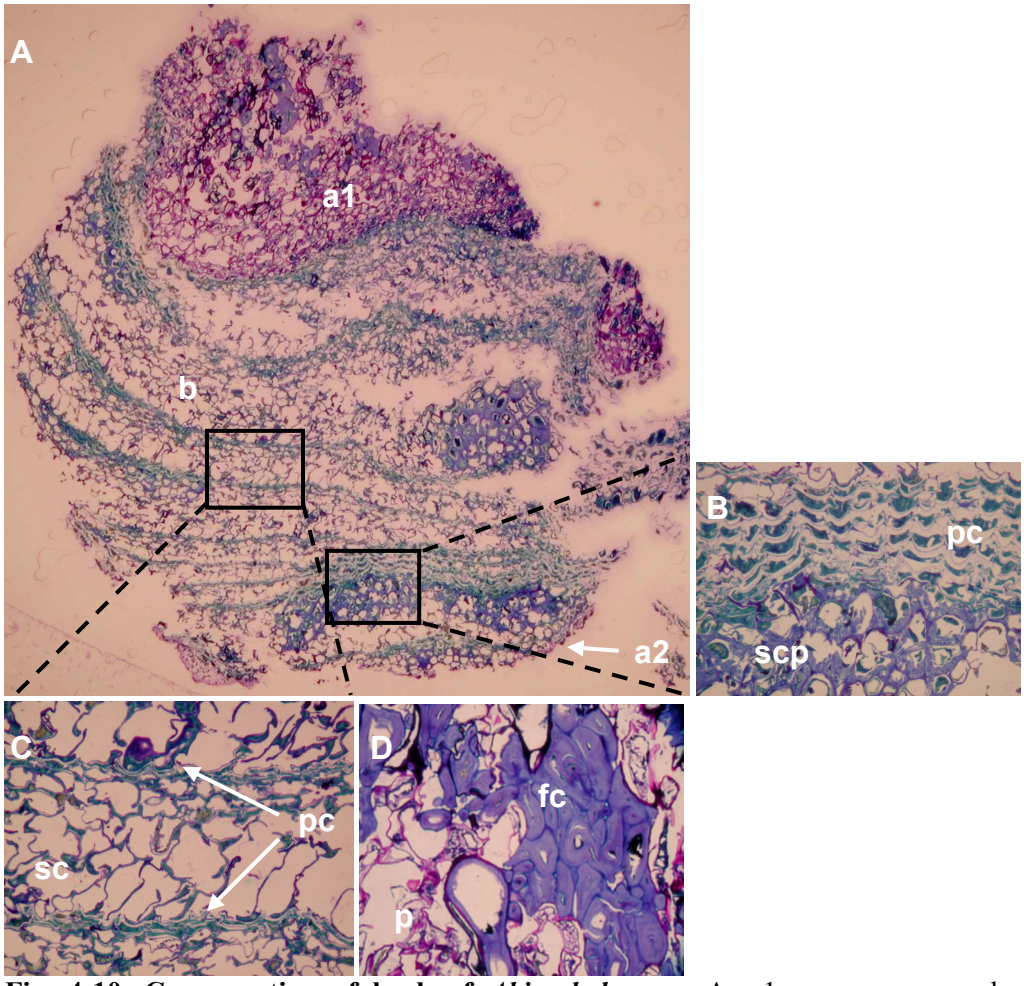

Fig. 4-10. Cross section of bark of *Abies balsamea*. A. a1: younger parenchyma, a2: rests of older parenchyma, b: layers of periderm. B. pc: phlobaphene cork, scp: sclerotic phelloid. C. pc: one layer of phlobaphene cork, sc: spongy cork. D. fc: fibre cell, p: parenchyma partly disrupted; D is no part of A.

4.3.3.1 Influence of tree species on element content of the bark

In lumina of fibre cells, no differences between the two tree species were found (Tab. 4-7), but concentrations of Al and Si in the secondary cell wall of the inner bark were higher in *Picea rubens* than in *Abies balsamea* (Tab. 4-8). In fir, higher concentrations of Cl, K, and Ca were found. In the outer bark, lumina of phlobaphene cork contained more Mg, Al, P, Cl, K, Ca, and Mn in *Abies* than in *Picea* (Tab. 4-9), whereas higher concentrations occurred in primary cell walls of *Picea rubens* for Mg, Si, and Ca; concentrations of S and Cl were higher in *Abies balsamea* (Tab. 4-10). Lumina of the cortex parenchyma in the outer bark showed higher values of Mg, S, K, and Mn in *Abies balsamea*, whereas in *Picea rubens* only Si was significantly higher (Tab. 4-11). The cell wall showed higher element concentrations of Mg, P, Cl, K, Ca, and Mn in *Abies* compared to *Picea* (Tab. 4-12). In the inner bark, lumina of sclerotic phelloids had a higher Si content in *Picea rubens* and a higher K content in *Abies balsamea* than the other tree species, respectively (Tab. 4-13). Also spongy cork cells of the outer bark showed differences in element contents between the two types of trees. Crystals (Fig. 4-11) located in the spongy cork of fir and spruce contained much higher amounts of Mn in fir (2061 mmol dm^{-3}) compared to spruce (1 mmol dm^{-3}; Tab. 4-14). Mn occurred also in higher concentrations in the primary cell wall of the spongy cork cells in *Abies* (Tab. 4-15).

A two-way analysis of variance (ANOVA) with the variables 'tree species' and 'cell type' revealed that the content of all elements was influenced mostly by 'cell type', whereby r^2 was ≥ 40 % for Mg, P, S, K, Ca, and Mn (Tab. 4-A44).

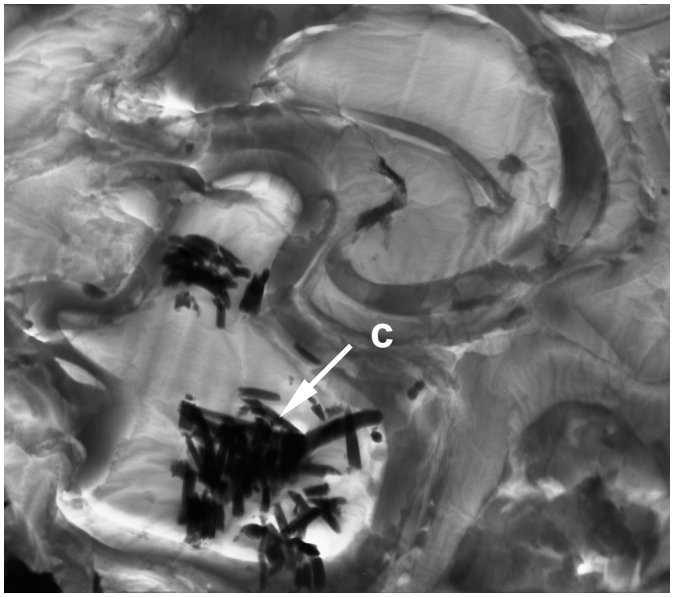

Fig. 4-11. Mn-crystals (c) in spongy cork cells of the outer part of the bark of *Abies balsamea*.

4.3.3.2 Element distribution in inner and outer bark of *Abies balsamea*

In the lumina of phlobaphene cork cells, higher concentrations of Mg, P, K, Ca, and Mn occurred in the outer bark than in the inner one (Tab. 4-9), whereas Na and K were more highly concentrated in the secondary cell wall of the inner bark (Tab. 4-10). Lumina of the cortex parenchyma of the inner bark had higher contents of Al and Ca, whereas more S and Mn were found in the outer layer (Tab. 4-11); the same was true for Mg, Si, P, S, Ca, and Mn in the cell wall of the outer bark (Tab. 4-12). In the lumina of sclerotic phelloids of the outer bark, near the cell wall, precipitates were investigated, containing high amounts of Mn, K, and P (Tab. 4-13). Lumina themselves had a high K content in the outer and inner bark; Ca and Cl occurred in high concentrations only in the inner layers. Secondary cell walls of sclerotic phelloids of the inner bark contained very low concentrations of Mn.

Tab. 4-7. Element content [mmol dm^{-3}] in fibre cell lumina of inner and outer bark of *Abies balsamea* and inner bark of *Picea rubens*.

	A. balsamea		*P. rubens*
	Fibre cell, lumen, outer bark	Fibre cell, lumen, inner bark	Fibre cell, lumen, inner bark
Na	9.08 ± 15.7	0.00 ± 0.00	0.00 ± 0.00
Mg	27.9 ± 10.0	8.89 ± 3.44	0.00 ± 0.00
Al	18.9 ± 17.1	5.98 ± 5.37	10.9 ± 4.61
Si	13.6 ± 13.9	12.6 ± 2.12	15.1 ± 6.28
P	18.9 ± 10.7	5.84 ± 2.21	0.00 ± 0.00
S	14.0 ± 4.34	10.0 ± 4.60	13.2 ± 7.06
Cl	7.09 ± 6.15	88.6 ± 135	5.18 ± 3.22
K	299 ± 147	45.6 ± 24.2	3.65 ± 5.15
Ca	262 ± 419	42.8 ± 28.9	17.6 ± 24.9
Fe	-	-	6.79 ± 0.24
Mn	388 ± 303	5.67 ± 2.16	1.52 ± 0.21

Arithmetic mean ± standard deviation. Statistics: U-test; $p \leq 0.05$. No significant differences occurred between data of *A. balsamea* nor between *A. balsamea* and *P. rubens*. *A. balsamea*: outer bark n = 3, inner bark: n = 3; *P. rubens*: n = 2.

Tab. 4-8. Element content [mmol dm^{-3}] in primary and secondary fibre cell walls of inner bark of *Abies balsamea* and *Picea rubens*.

	A. balsamea		*P. rubens*	
	Fibre cell, primary cell wall, inner bark	Fibre cell, secondary cell wall, inner bark	Fibre cell, secondary cell wall, inner bark	*Abies/Picea*
Na	0.00 ± 0.00	6.75 ± 21.3	2.76 ± 3.23	
Mg	7.01 ± 1.27	3.18 ± 4.31	4.05 ± 2.87	
Al	2.06 ± 2.91	1.79 ± 2.64	7.42 ± 1.74	**
Si	3.16 ± 0.35	5.26 ± 2.64	16.6 ± 2.04	**
P	0.00 ± 0.00	1.00 ± 1.29	0.00 ± 0.00	
S	2.25 ± 3.17	0.84 ± 1.26	0.00 ± 0.00	
Cl	16.4 ± 9.11	38.9 ± 97.2	2.89 ± 3.85	*
K	34.5 ± 20.6	26.3 ± 26.4	1.66 ± 3.31	**
Ca	32.2 ± 25.5	15.8 ± 16.1	2.85 ± 2.97	**
Fe	-	-	4.28 ± 0.70	-
Mn	3.57 ± 2.59	1.32 ± 1.73	1.25 ± 0.86	

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, dash: no statistics carried out. *A. balsamea*: primary cell wall: n = 2, secondary cell wall: n = 13; *P. rubens*: n = 4.

Tab. 4-9. Element content [mmol dm^{-3}] in lumina of phlobaphene cork of inner and outer bark of *Abies balsamea* and outer bark of *Picea rubens*.

	A. balsamea			*P. rubens*	
	Phlobaphene cork, lumen, inner bark	Phlobaphene cork, lumen, outer bark	Inner/outer bark	Phlobaphene cork, lumen, outer bark	*Abies/Picea*
Na	20.9 ± 25.5	155 ± 419		1.37 ± 3.06	
Mg	1.15 ± 3.63	11.8 ± 12.1	*	0.00 ± 0.00	*
Al	19.6 ± 18.4	29.4 ± 38.1		7.65 ± 2.03	*
Si	7.31 ± 4.87	11.6 ± 8.53		7.19 ± 1.89	
P	0.97 ± 2.08	4.93 ± 4.70	*	0.00 ± 0.00	*
S	6.65 ± 5.35	10.2 ± 11.7		2.23 ± 2.36	
Cl	23.7 ± 22.0	166 ± 464		1.09 ± 1.10	**
K	38.0 ± 22.7	109 ± 73.4	**	0.40 ± 0.89	***
Ca	46.0 ± 44.5	122 ± 83.1	*	0.75 ± 1.67	***
Fe	-	-	-	2.60 ± 0.69	
Mn	12.4 ± 11.8	69.2 ± 59.2	***	0.93 ± 0.69	***

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, dash: no statistics carried out. *A. balsamea*: inner bark: n = 10, outer bark: n = 18; *P. rubens*: n = 5.

Tab. 4-10. Element content [mmol dm^{-3}] in primary and secondary cell wall of phlobaphene cork of inner and outer bark of *Abies balsamea* and *Picea rubens*.

	A. balsamea	*P. rubens*		*A. balsamea*		
	Phlobaphene cork, primary cell wall, outer bark	Phlobaphene cork, primary cell wall, outer bark	*Abies/Picea*	Phlobaphene cork, secondary cell wall, outer bark	Phlobaphene cork, secondary cell wall, inner bark	Inner/outer bark
Na	30.0 ± 39.6	1.33 ± 2.65		0.00 ± 0.00	11.9 ± 10.1	*
Mg	0.46 ± 1.58	6.77 ± 3.07	***	0.00 ± 0.00	0.66 ± 1.48	
Al	6.44 ± 4.27	6.90 ± 0.40		5.11 ± 3.58	6.53 ± 2.63	
Si	10.1 ± 8.01	18.1 ± 3.52	*	8.82 ± 3.76	7.51 ± 3.29	
P	0.96 ± 2.24	0.67 ± 1.34		1.75 ± 2.40	1.33 ± 2.02	
S	20.1 ± 9.55	2.19 ± 2.54	*	2.27 ± 3.13	5.20 ± 2.60	
Cl	34.2 ± 29.5	4.26 ± 1.20	**	8.78 ± 6.88	15.0 ± 10.8	
K	11.6 ± 11.7	2.82 ± 1.07		0.00 ± 0.00	4.59 ± 2.96	**
Ca	23.4 ± 39.8	59.2 ± 34.2	**	1.05 ± 2.34	1.90 ± 0.86	
Fe	-	2.34 ± 0.23	-	-	-	-
Mn	5.78 ± 7.80	2.84 ± 0.83		0.00 ± 0.00	0.30 ± 0.68	

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, dash: no statistics carried out. *A. balsamea*: primary cell wall: n = 12, secondary cell wall, each outer and inner bark: n = 5; *P. rubens*: n = 4.

Tab. 4-11. Element content [mmol dm^{-3}] in lumina of cortex parenchyma of inner and outer bark of *Abies balsamea* and *Picea rubens*.

	A. balsamea			*P. rubens*	
	Cortex parenchyma, lumen, inner bark	Cortex parenchyma, lumen, outer bark	Inner/outer bark	Cortex parenchyma, lumen, outer bark	*Abies/Picea*
Na	0.60 ± 2.52	2.10 ± 4.46		2.36 ± 5.28	
Mg	20.7 ± 21.0	23.0 ± 12.6		6.17 ± 5.85	*
Al	11.3 ± 7.60	3.70 ± 5.36	*	5.02 ± 2.88	
Si	4.36 ± 4.70	7.74 ± 5.78		21.2 ± 3.20	**
P	8.67 ± 9.37	94.4 ± 177		3.18 ± 4.62	
S	10.5 ± 4.07	36.2 ± 30.6	**	11.3 ± 4.07	*
Cl	10.0 ± 9.66	6.39 ± 4.04		3.84 ± 1.73	
K	129 ± 33.5	97.9 ± 40.5		2.94 ± 2.30	**
Ca	30.5 ± 104	26.6 ± 34.1	**	25.2 ± 25.2	
Fe	-	-	-	3.31 ± 2.53	-
Mn	8.84 ± 8.04	35.3 ± 47.4	*	3.01 ± 1.96	*

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, dash: no statistics carried out. *A. balsamea*: inner bark: n = 18, outer bark: n = 10; *P. rubens*: n = 5.

Tab. 4-12. Element content [mmol dm^{-3}] in the cell wall of cortex parenchyma of inner and outer bark of *Abies balsamea* and *Picea rubens*.

	A. balsamea			*P. rubens*	
	Cortex parenchyma, cell wall, inner bark	Cortex parenchyma, cell wall, outer bark	Inner/outer bark	Cortex parenchyma, cell wall, outer bark	*Abies/Picea*
Na	3.90 ± 8.51	6.36 ± 8.89		2.78 ± 4.52	
Mg	15.9 ± 9.86	34.4 ± 20.9	*	5.43 ± 4.02	**
Al	4.08 ± 4.65	2.85 ± 5.14		4.46 ± 3.41	
Si	5.67 ± 5.13	11.7 ± 6.76	*	21.9 ± 17.9	
P	17.8 ± 13.4	38.6 ± 22.9	*	0.32 ± 0.72	**
S	4.85 ± 4.76	9.92 ± 9.33	*	6.85 ± 3.16	
Cl	13.5 ± 7.23	13.0 ± 8.05		5.26 ± 2.82	*
K	122 ± 49.9	146 ± 49.6		3.42 ± 1.06	**
Ca	196 ± 142	660 ± 378	**	45.1 ± 22.4	**
Fe	-	-	-	2.35 ± 1.31	-
Mn	15.8 ± 9.68	46.7 ± 25.1	**	4.58 ± 2.84	**

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, dash: no statistics carried out. *A. balsamea*: inner bark: n = 14, outer bark: n = 13; *P. rubens*: n = 5.

Tab. 4-13. Element content [mmol dm^{-3}] in secondary cell wall, lumina and in deposition near the cell wall in the lumina of sclerotic phelloids of inner and outer bark of *Abies balsamea* and *Picea rubens*.

	A. balsamea					*P. rubens*	
	Sclerotic phelloid, deposition, outer bark	Sclerotic phelloid, secondary cell wall, inner bark	Sclerotic phelloid, lumen, outer bark	Sclerotic phelloid, lumen, inner bark	Inner/outer bark, lumen	Sclerotic phelloid, lumen, inner bark	*Abies/Picea*
Na	0.00 ± 0.00	1.45 ± 4.11	2.09 ± 2.96	9.70 ± 11.83	-	7.35 ± 7.80	
Mg	17.1 ± 21.7	1.91 ± 2.64	24.8 ± 2.31	5.74 ± 7.91	-	1.80 ± 3.11	
Al	5.08 ± 6.33	0.00 ± 0.00	10.5 ± 1.00	7.19 ± 8.94	-	20.8 ± 12.2	
Si	8.09 ± 2.70	8.55 ± 2.12	8.75 ± 3.36	13.5 ± 5.05	-	69.8 ± 43.7	*
P	70.3 ± 17.6	0.55 ± 1.18	5.32 ± 1.01	4.27 ± 4.52	-	0.00 ± 0.00	
S	3.05 ± 5.29	0.23 ± 0.65	8.31 ± 3.15	13.0 ± 8.04	-	11.9 ± 5.81	
Cl	10.1 ± 1.57	6.41 ± 3.19	3.52 ± 0.10	57.6 ± 58.0	-	55.6 ± 44.6	
K	125 ± 32.8	14.9 ± 2.95	117 ± 8.59	59.6 ± 18.7	-	17.5 ± 15.6	*
Ca	5.13 ± 2.56	8.70 ± 2.63	3.83 ± 0.35	78.9 ± 74.2	-	45.9 ± 36.9	
Fe	-	-	-	-	-	14.3 ± 2.06	-
Mn	1774 ± 1042	0.67 ± 0.95	4.22 ± 0.49	7.65 ± 6.56	-	0.19 ± 0.33	

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, dash: no statistics carried out. *A. balsamea*: deposition: n = 3, secondary cell wall: n = 8, lumen outer bark: n = 2, lumen inner bark: n = 8; *P. rubens*: n = 3.

Tab. 4-14. Element content [mmol dm^{-3}] in lumina and in crystals deposited in the lumina of spongy cork of outer bark of *Abies balsamea* and *Picea rubens*.

	A. balsamea	*P. rubens*		*A. balsamea*	*P. rubens*	
	Spongy cork, crystals, outer bark	Spongy cork, crystals, outer bark	*Abies/Picea*	Spongy cork, lumen, outer bark	Spongy cork, lumen, outer bark	*Abies/Picea*
Na	1.98 ± 5.23	226 ± 412	**	1.10 ± 3.48	0.00 ± 0.00	
Mg	17.9 ± 18.6	1.15 ± 2.58	*	5.83 ± 6.02	3.39 ± 4.95	
Al	7.75 ± 11.4	18.3 ± 9.00	*	10.5 ± 4.88	8.59 ± 4.89	
Si	2.43 ± 4.16	98.4 ± 46.6	**	13.6 ± 10.6	19.6 ± 5.40	
P	23.8 ± 36.6	1.18 ± 2.64	*	13.6 ± 12.6	0.00 ± 0.00	**
S	0.52 ± 1.38	25.0 ± 3.89	**	2.96 ± 1.83	7.87 ± 5.19	
Cl	17.3 ± 23.8	374 ± 583	**	6.29 ± 3.09	6.83 ± 6.03	
K	24.8 ± 23.7	25.2 ± 20.2		57.0 ± 52.6	4.72 ± 6.03	**
Ca	78.0 ± 195	93.0 ± 86.8	*	35.4 ± 49.5	5.89 ± 4.41	
Fe	-	44.4 ± 67.1	-	-	4.75 ± 1.11	-
Mn	2061 ± 1349	1.18 ± 1.29	**	94.3 ± 34.8	1.36 ± 1.26	**

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, dash: no statistics carried out. *A. balsamea*: crystals: n = 7, lumen: n = 10; *P. rubens*: crystals: n = 5, lumen: n = 5.

Tab. 4-15. Element content [mmol dm^{-3}] in primary cell wall of spongy cork of outer bark of *Abies balsamea* and *Picea rubens*.

	A. balsamea	*P. rubens*	
	Spongy cork, primary cell wall, outer bark	Spongy cork, primary cell wall, outer bark	*Abies/Picea*
Na	0.59 ± 1.66	7.02 ± 11.5	
Mg	0.00 ± 0.00	3.84 ± 5.50	
Al	0.00 ± 0.00	5.15 ± 4.85	*
Si	10.1 ± 16.1	20.7 ± 4.27	*
P	0.00 ± 0.00	0.53 ± 1.18	
S	19.4 ± 14.1	13.2 ± 2.54	
Cl	24.0 ± 16.4	11.1 ± 10.7	
K	4.54 ± 3.88	2.72 ± 4.34	
Ca	11.5 ± 6.43	9.30 ± 9.02	
Fe	-	5.13 ± 0.99	-
Mn	20.8 ± 9.17	2.30 ± 0.56	**

Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance:
* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$, dash: no statistics carried out.
A. balsamea: n = 8; *P. rubens*: n = 5.

4.3.4 Water-holding capacity

Mean water-holding capacity of the bark did not differ significantly between the two tree species nor did the vitality of the trees influence it (Tab. 4-16). The mean was even slightly higher on living than on dead trees. The range was wider for living trees than dead ones and wider for *Abies balsamea* than *Picea rubens* (Tab. 4-A45). Coefficient of variation was higher on *Abies balsamea* than on *Picea rubens*, but did not show a consistent tendency for the comparison between living versus dead trees within the two species (Tab. 4-16). Dead *Picea rubens* had a higher coefficient of variation than the living one, whereas dead *Abies balsamea*'s coefficient was lower than the living counterpart.

Tab. 4-16. Water-holding capacity in the bark of living (B) and dead (DB) *Abies balsamea* and living (R) and dead (DR) *Picea rubens*.

	Water-holding capacity [%]	Coefficient of variation [%]
R	70.2 ± 17.4	14.52
DR	62.9 ± 9.14	24.83
B	72.1 ± 30.7	42.53
DB	63.3 ± 22.2	35.03

Water-holding capacity: arithmetic mean ± standard deviation; Statistics: t-test, $p \leq 0.05$. n = 15.

Within *Picea rubens*, water-holding capacity increased slightly from vitality class V to III, then decreased from III to II. From class II to I capacity increased again (Fig. 4-12). In contrast, water-holding capacity at *Abies balsamea* decreased slightly from V to IV. Vitality class III was not represented in the randomly selected sample size. Capacity was raised slightly from IV to II, then decreased from II to I. As the sample size was a too small in vitality classes IV, III, and II for *Picea rubens* as well as in vitality classes III and II for *Abies balsamea*, statistics was not carried out.

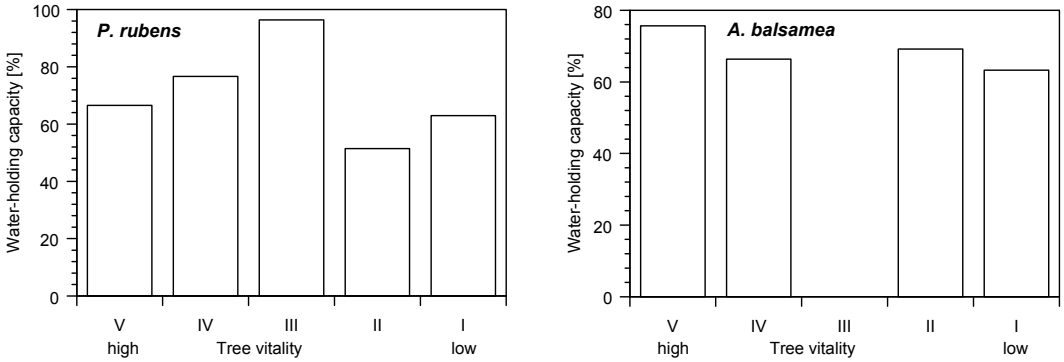

Fig. 4-12. Water-holding capacity of *Picea rubens* and *Abies balsamea* separated after vitality classes. N: *A. balsamea*: class V = 9, IV = 5, III = 0, II = 1, I = 15; *P. rubens*: class V = 11, IV = 1, III = 2, II = 1, I = 15.

4.3.5 Correlations between investigated element contents of the bark

Results of Spearman correlation matrices are presented separately for every type of tree in Tab. 4-A46 – 4-A49 in the appendix. Only few strong correlations ($r^2 \geq 50$ %) occurred between concentrations of N and Cu as well as between pH and conductivity for living *Picea rubens*. Dead *Picea rubens* showed correlations between concentrations of Ca and Zn. More parameters were intercorrelated in the bark of *Abies balsamea* with $r^2 \geq 50$ %. In living fir, C was correlated with Ca, as was K with Mg, Mn with Zn as well as pH with conductivity, Mg, and Fe. On dead *Abies balsamea*, Ca correlated with Mg and Zn, Mg and Mn with Zn. Ca, Mg, Mn, and Zn all correlated with pH.

4.4 Microclimate

Mean light intensity and evaporation were not different between either of the types of trees (Tab. 4-17). When analysed separately for each sample day, only in a few cases light (on two days) and evaporation data (on eight days) differed between *Abies balsamea* and *Picea rubens* (Tab. 4-A50 - Tab. 4-A51).

Tab. 4-17. Mean light intensity and evaporation of living (R) and dead (DR) *Picea rubens* as well as of living (B) and dead (DB) *Abies balsamea*.

	R	DR	B	DB
PPFD [%], n = 60[a]	18.2 ± 5.4	17.9 ± 4.8	17.9 ± 5.8	19.1 ± 3.6
n = 99[b]	14.0 ± 4.4	16.6 ± 6.0	15.7 ± 6.0	15.2 ± 3.5
Evaporation [ml dm^{-2} d^{-1}]	10.3 ± 1.9	10.5 ± 2.5	10.1 ± 1.9	8.7 ± 2.2

Arithmetic mean ± standard deviation. No significant differences (light: U-test, evaporation: t-test; $p \leq 0.05$). Light: [a] Mean values of 12 days; [b] Mean values of 3 days. Evaporation: n = 10, measured for one month.

Measuring the diurnal variation of relative humidity and temperature gave a minimum in the afternoon hours for the former one, whereas the latter one as well as evaporation had a maximum at the same time (Fig. 4-13, Fig. 4-14). Lower relative humidity occurred only in the afternoon between *Abies balsamea* and *Picea rubens*.

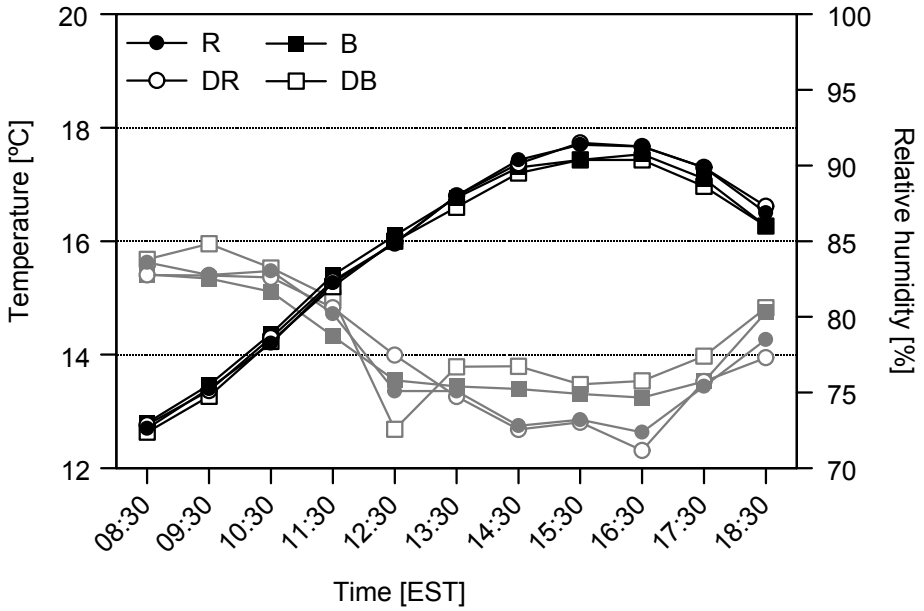

Fig. 4-13. Diurnal variation of relative humidity and air temperature. n = 3, measured for 5 to 6 days.

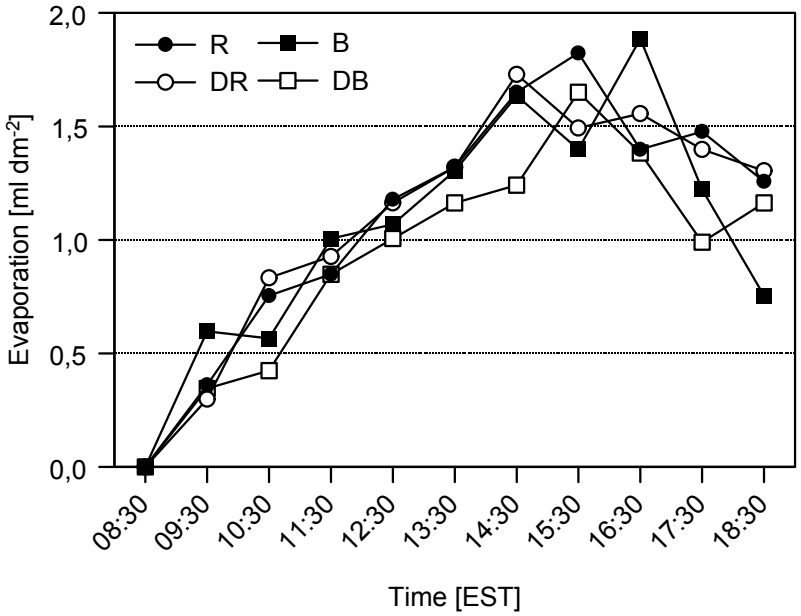

Fig. 4-14. Diurnal variation of evaporation. n = 3, measured for 5 to 6 days.

4.5 Experimental studies to the NO_3^- sensitivity of *Hypogymnia physodes*

Concentrations of chlorophylls a and b as well as of phaeophytins a and b decreased with increasing NO_3^- concentration of the incubation medium (Fig. 4-15, Tab. 4-18). The decrease was statistically significant for chlorophyll a and for phaeophytin a for concentrations of 100 µmol NO_3^- and higher; for chlorophyll b and phaeophytin b the significant difference occurred at concentrations of 1 mM NO_3^- and more. The controls did not differ between pH 4 and 6.

The concentrations of ergosterol were not affected by any treatment (Tab. 4-18).

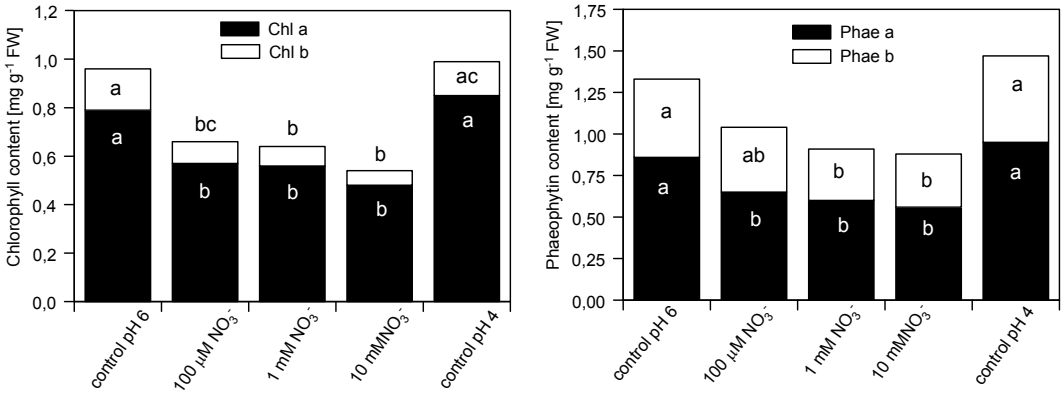

Fig. 4-15. Chlorophyll and phaeophytin contents of *Hypogymnia physodes* after one week treatment with nitrate.

Tab. 4-18. Chlorophyll a, b, phaeophytin a, b, and ergosterol content in *Hypogymnia physodes* after one week treatment with nitrate.

	Control pH 6	100 µM NO_3^-	1 mM NO_3^-	10 mM NO_3^-	Control pH 4
Chl a [mg g^{-1} FW]	0.79 ± 0.18a	0.57 ± 0.14b	0.56 ± 0.10b	0.48 ± 0.13b	0.85 ± 0.23a
Chl b [mg g^{-1} FW]	0.17 ± 0.04a	0.09 ± 0.06bc	0.08 ± 0.06b	0.06 ± 0.04b	0.14 ± 0.07ac
Phae a [mg g^{-1} FW]	0.86 ± 0.17a	0.65 ± 0.18b	0.60 ± 0.11b	0.56 ± 0.16b	0.95 ± 0.26a
Phae b [mg g^{-1} FW]	0.47 ± 0.10a	0.39 ± 0.18b	0.31 ± 0.08b	0.32 ± 0.12ab	0.52 ± 0.18a
Ergosterol [mg g^{-1} DW]	1.29 ± 0.40a	1.19 ± 0.18a	1.19 ± 0.28a	1.13 ± 0.23a	1.09 ± 0.23a
Chl a : Ergosterol	0.61	0.48	0.47	0.42	0.78

Arithmetic means ± standard deviation. Statistics: t-test; $p \leq 0.05$. n = 10.

Algal cells as well as fungal hyphae of medulla and upper cortex did not show any structural differences between the different NO_3^- treatments or between the controls at different pH values when studied with SEM (Fig. 4-16, Fig. 4-17).

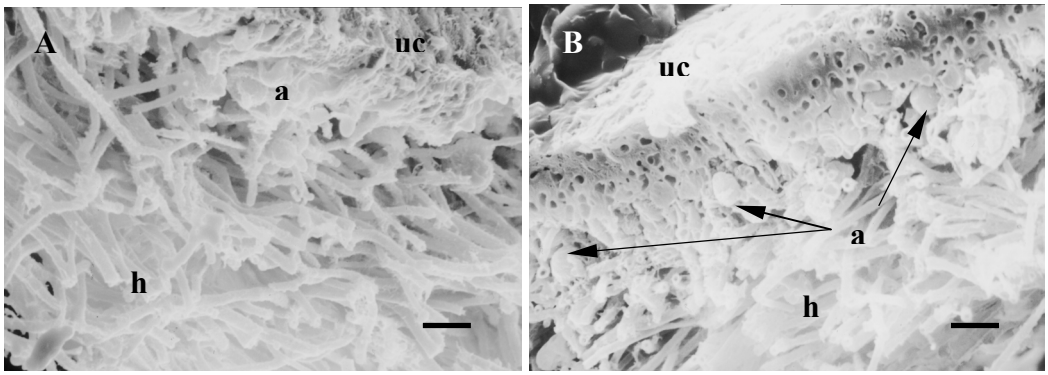

Fig. 4-16. Thalli cross sections of *Hypogymnia physodes*. A. control pH 4, B. Subsequent to one week treatment with 10 mM NO_3^-. a. algal cells, h. hyphae, uc. upper cortex. Bar: 10 µm.

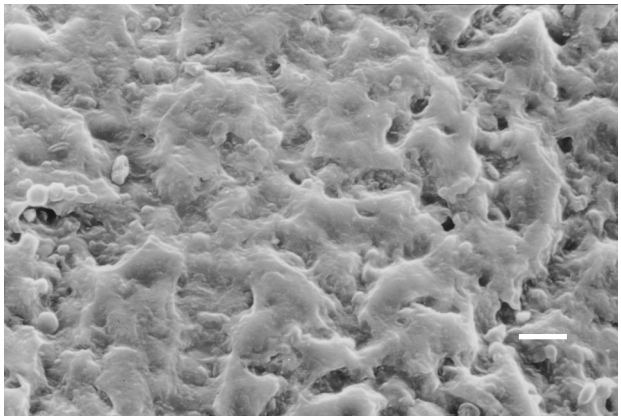

Fig. 4-17. Upper cortex of *Hypogymnia physodes*. Subsequent to one week treatment with 10 mM NO_3^-. As a reference for a not affected cortex consider e.g. GLIEMEROTH (1990). Bar: 10 µm.

4.6 Soil

Organic matter could be divided into L and O_f layer, whereby the former was 2 mm thick and consisted predominantly of dead needles. The structure was loose without root penetration. The O_f layer, also consisting of dead needles, was up to 5.7 cm thick with a loose structure, whereas root penetration was very high compared to the L layer.

The mineral soil could be divided into an A and C horizon. The A horizon was up to 32.5 cm deep, with a dark brown color, indicating a very high content of humus. The structure was crumb to granular, the density low. Root penetration was high to very high. No rocks from the C horizon were found in the A horizon. C occurred below 32.5 cm. Recorded soil properties led to the conclusion that Inceptisol is the predominant type of soil on the field site. Data of the soil chemistry are compiled in Tab. 4-19.

Tab. 4-19. Element content in the soil.

	Extraction medium	Horizon	
N [mol kg^{-1} DW]	Total content	O_f	1.42 ± 0.09
	Total content	A	0.94 ± 0.24
C [mol kg^{-1} DW]	Total content	O_f	40.9 ± 1.43
	Total content	A	23.0 ± 5.22
K [mmol kg^{-1} DW]	HCl	O_f	10.1 ± 1.22
	$BaCl_2$	A	1.33 ± 0.43
Ca [mmol kg^{-1} DW]	HCl	O_f	42.8 ± 6.91
	$BaCl_2$	A	4.67 ± 2.56
Mg [mmol kg^{-1} DW]	HCl	O_f	7.05 ± 1.12
	$BaCl_2$	A	0.83 ± 0.36
Fe [mmol kg^{-1} DW]	HCl	O_f	32.6 ± 5.43
	$BaCl_2$	A	3.94 ± 0.65
Mn [mmol kg^{-1} DW]	HCl	O_f	1.09 ± 0.26
	$BaCl_2$	A	0.08 ± 0.04
Al [mmol kg^{-1} DW]	HCl	O_f	56.4 ± 8.49
	$BaCl_2$	A	61.1 ± 12.2
Zn [mmol kg^{-1} DW]	HCl	O_f	0.98 ± 0.23
	$BaCl_2$	A	0.17 ± 0.11
pH	H_2O	O_f	3.18 ± 0.10
	H_2O	A	3.51 ± 0.28
pH	KCl	O_f	2.39 ± 0.05
	KCl	A	3.10 ± 0.30

Arithmetic mean ± standard deviation. Statistics: U-Test; $p \leq 0.05$. n = 20.

4.7 Relations between chemical site factors and epiphytic lichen vegetation

4.7.1 Stem flow

Cover of several lichen species decreased with increasing NO_3^-, S, Ca, and Mn content of stem flow (Tab. 4-20). Except for *Arthonia caesia* and *Cladonia coniocraea*, cover of all species occurring on more than 50 % of the sample trees correlated with NO_3^-. In 1999 cover of 12 epiphytes decreased with increasing NO_3^- concentration, whereas in 2000 14 decreased with increasing NO_3^-. When mean NO_3^- content was more than 10 µmol l^{-1} in 1999, lichen cover did not exceed 1 % (Fig. 4-18). In 2000 mean NO_3^- concentration was much lower than in 1999. Instead of approximately up to 40 µmol l^{-1} a concentration of only up to 4 µmol l^{-1} was measured.

In contrast to NO_3^-, cover of much fewer lichens decreased with increasing S, Ca, or Mn content (Tab. 4-20). In 1999 only one species (*Cladonia coniocraea*), 2000 two species (*Parmelia saxatilis*, *Micarea prasina*) correlated with S, whereas with Mn no lichen at all showed any influence in 1999, but four (*Mycoblastus sanguinarius, Platismatia glauca, Parmelia saxatilis,* and *Micarea prasina*) in 2000. Also Ca was not correlated with any lichen in 1999, but with seven species in 2000. In the case of Mn lichen cover, except for one lichen species (*Micarea prasina*), was less than 1 % when the element content exceeded 10 µmol l^{-1} (Fig. 4-19). *Micarea prasina* reached a cover of up to 4 % at a Mn concentration of 18 µmol l^{-1}. S and Ca instead did not show this restriction of lichen cover to element concentration. In the former case, for instance, cover could vary from approximately 1 % (*Parmelia saxatilis*) to 10 % (*Cladonia coniocraea*) at 15 µmol l^{-1} (Fig. 4-19). In one case lichen cover correlated negatively with Fe (*Cladonia coniocraea* in 1999; $r = -0.45$, $p \leq 0.01$), in another case with Mg (*Parmelia saxatilis* in 2000; $r = -0.32$, $p \leq 0.05$).

Tab. 4-20. Correlation between lichen cover and element concentrations in stem flow.

	Year	NO_3^-	S	Ca	Mn
Alectoria sarmentosa	1999	-0.46**	.	.	.
	2000	-0.47**	.	.	.
Bryoria fuscescens	1999	-0.38*	.	.	.
	2000	-0.40*	.	.	.
Cladonia pyxidata s.l.	1999	-0.36*	.	.	.
	2000	-0.42**	.	.	.
Cladonia squamosa	1999	.	.	.	.
	2000	-0.36*	.	.	.
Evernia mesomorpha	1999	.	.	.	.
	2000	-0.43**	.	.	.
Imshaugia aleurites	1999	-0.35*	.	.	.
	2000	-0.37*	.	.	.
Lecidea nylanderi	1999	-0.51*	.	.	.
	2000	-0.40*	.	.	.
Pseudevernia cladonia	1999	-0.52***	.	.	.
	2000	-0.59***	.	.	.
Flavopunctelia soredica	1999	-0.45*	.	.	.
	2000	-0.42**	.	-0.31*	.
Hypogymnia physodes	1999	-0.56***	.	.	.
	2000	-0.51**	.	-0.42**	.
Lepraria jackii	1999	-0.63**	.	.	.
	2000	.	.	-0.51**	.
Usnea spec.	1999	-0.57***	.	.	.
	2000	-0.54***	.	-0.49**	.
Mycoblastus sanguinarius	1999	-0.42**	.	.	.
	2000	-0.38*	.	-0.37*	-0.46**
Platismatia glauca	1999	-0.36*	.	.	.
	2000	-0.33*	.	.	-0.34*
Parmelia saxatilis	1999	.	.	.	.
	2000	-0.35*	-0.37*	-0.38*	-0.57***
Micarea prasina	1999	.	.	.	.
	2000	.	-0.35*	-0.36*	-0.57***
Cladonia coniocraea	1999	.	-0.36*	.	.
	2000	.	.	.	.

Correlation coefficients calculated from mean concentrations of every sample tree over the entire measuring period. Regression: $y = a/(b*x)$. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. n = 40. Indifferent species are not listed in this table.

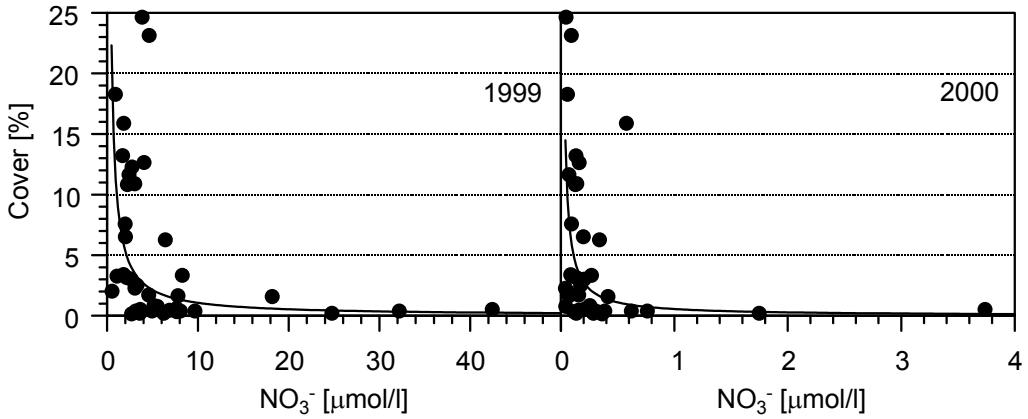

Fig. 4-18. Correlation between cover of *Hypogymnia physodes* and NO_3^- content in stem flow. Regression model: a/(b*x). 1999: n = 40; r = -0.56, $p \leq 0.001$. 2000: n = 39; r = -0.51, $p \leq 0.01$.

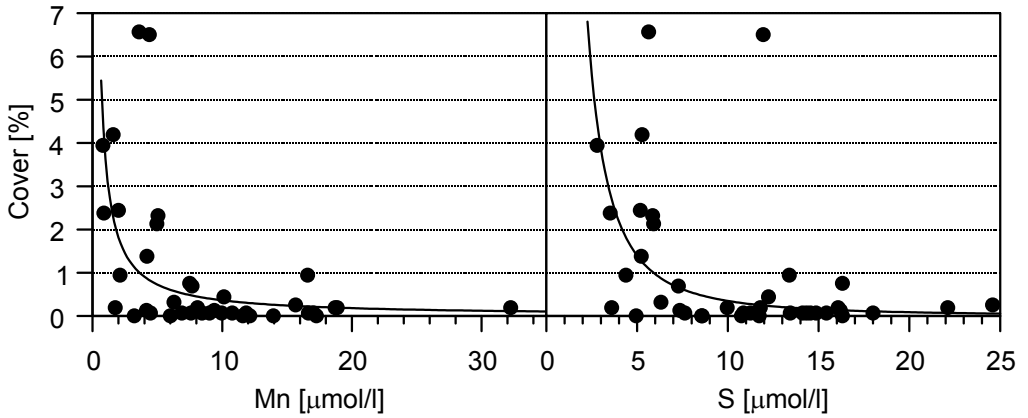

Fig. 4-19. Correlation between cover of *Parmelia saxatilis* and Mn as well as S content in stem flow of 2000. Regression model: a/(b*x). n = 39; Mn: r = -0.57, $p \leq 0.001$; S: r = -0.37, $p \leq 0.05$.

In some cases, cover correlated with more than one element (Tab. 4-20). Linear multiple regression analysis showed that the correlation coefficient found for NO_3^- in stem flow and lichen cover was not (*Flavopunctelia soredica*) or only slightly enhanced (*Hypogymnia physodes*, *Usnea* spec.) when Ca was included in the model (Tab. 4-A52). In the case of *Platismatia glauca*, Mn showed the same behaviour than Ca for *Hypogymnia physodes* and *Usnea* spec. Mn was most closely correlated with cover of *Mycoblastus sanguinarius* and *Parmelia saxatilis*, where NO_3^- as well as Mg only slightly increased the multiple correlation coefficient. S did not enhance the correlation coefficient in the case of *Parmelia saxatilis*, whereas with *Micarea prasina* and *Cladonia coniocraea* it was the most closely correlated element.

4.7.2 Bark properties

4.7.2.1 Correlation of lichen cover with total element content of bark

Weak negative correlations occurred with lichen cover and concentration of Fe and Mn in bark (Fig. 4-A1 – 4-A3). In contrast to the correlations with stem flow, nearly as many lichen species correlating with element content in the bark did not belong to the epiphytes occurring on over 50 % of the trees, such as *Alectoria sarmentosa*, *Bryoria capillaris*, *B. furcellata*, *B. nadvornikiana*, *Cladonia squamosa*, *Evernia mesomorpha*, and *Hypocenomyce friesii*. Cover of seven species decreased with increasing element content in the case of Fe (Fig. 4-A1), whereas nine species correlated with Mn (Fig. 4-A2 - Fig. 4-A3), but the coefficient of correlation never exceeded 0.33 (Fe) or 0.44 (Mn). *Pseudevernia cladonia* was the only lichen correlated with element concentrations of Fe and Mn. Linear multiple regression analysis was not calculated, as no satisfying linearization was found.

4.7.2.2 Correlation of lichen cover with different extractants

Correlations of element concentrations were calculated with the 10 most frequent lichen species (*Arthonia caesia*, *Cladonia coniocraea*, *Flavopunctelia soredica*, *Hypogymnia physodes*, *Imshaugia aleurites*, *Lecidea nylanderi*, *Lepraria jackii*, *Mycoblastus sanguinarius*, *Platismatia glauca*, and *Pseudevernia cladonia*), and with *Usnea* spec. as a sensitive lichen group.

Effects of extraction media on lichen cover can be seen best in correlations of *Arthonia caesia*. Therefore, graphs of this lichen are shown here to represent all other lichen species; for other correlations consider Fig. 4-A4 – 4-A8 and Tab. 4-A53 – Tab. 4-A56 in the appendix.

In general, water shows the lowest concentrations determined in the filtrate for every element (Fig. 4-20), acid digested total bark content the highest (Fig. 4-21). The element concentration of the total bark content and of the $SrCl_2$ extraction was similar high for K and Mg (Fig. 4-22 - Fig. 4-23). Also, the coefficient of correlation was higher with $SrCl_2$ (K: r = -0.36, Mg: r = -0.39) than with extraction media H_2O (K: r = -0.34, Mg: r = -0.32) or EDTA (K: r = -0.34, Mg: r = -0.36) for these elements. Ca on the other hand did not show any decisive difference between $SrCl_2$ and EDTA extraction (Fig. 4-21 - Fig. 4-22). Fe, Mn, Zn, and Cu showed the highest coefficients of correlation values with EDTA as an extraction media (Fig. 4-21). Compared to the total bark content, Fe and Cu are generally not well extracted from any of the media used (H_2O, EDTA, or $SrCl_2$), whereas Mn and Zn achieved similarly high concentrations with EDTA.

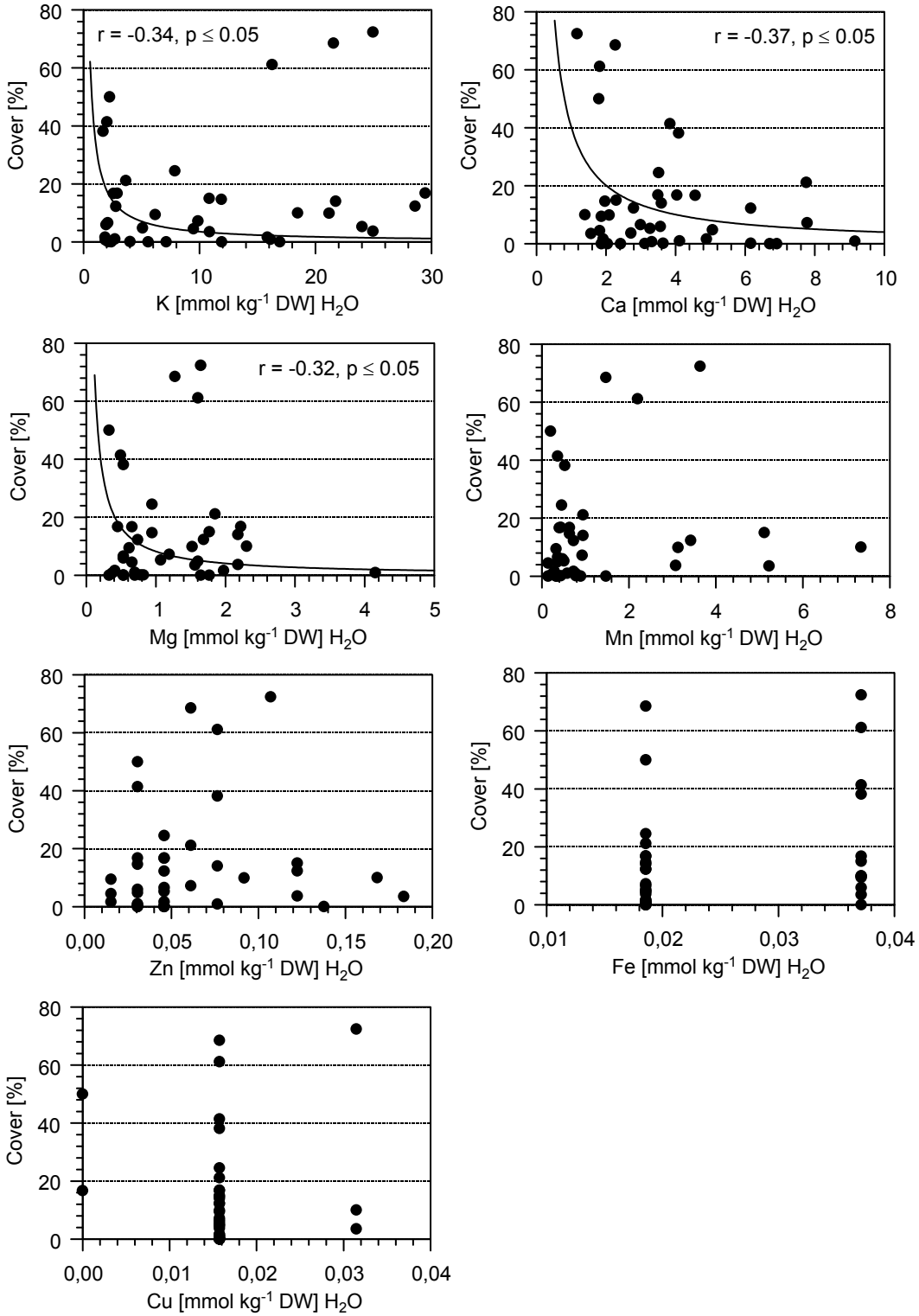

Fig. 4-20. Lichen cover of *Arthonia caesia* vs. element content of extraction with H_2O. Regression model: a/(b*x). n = 40.

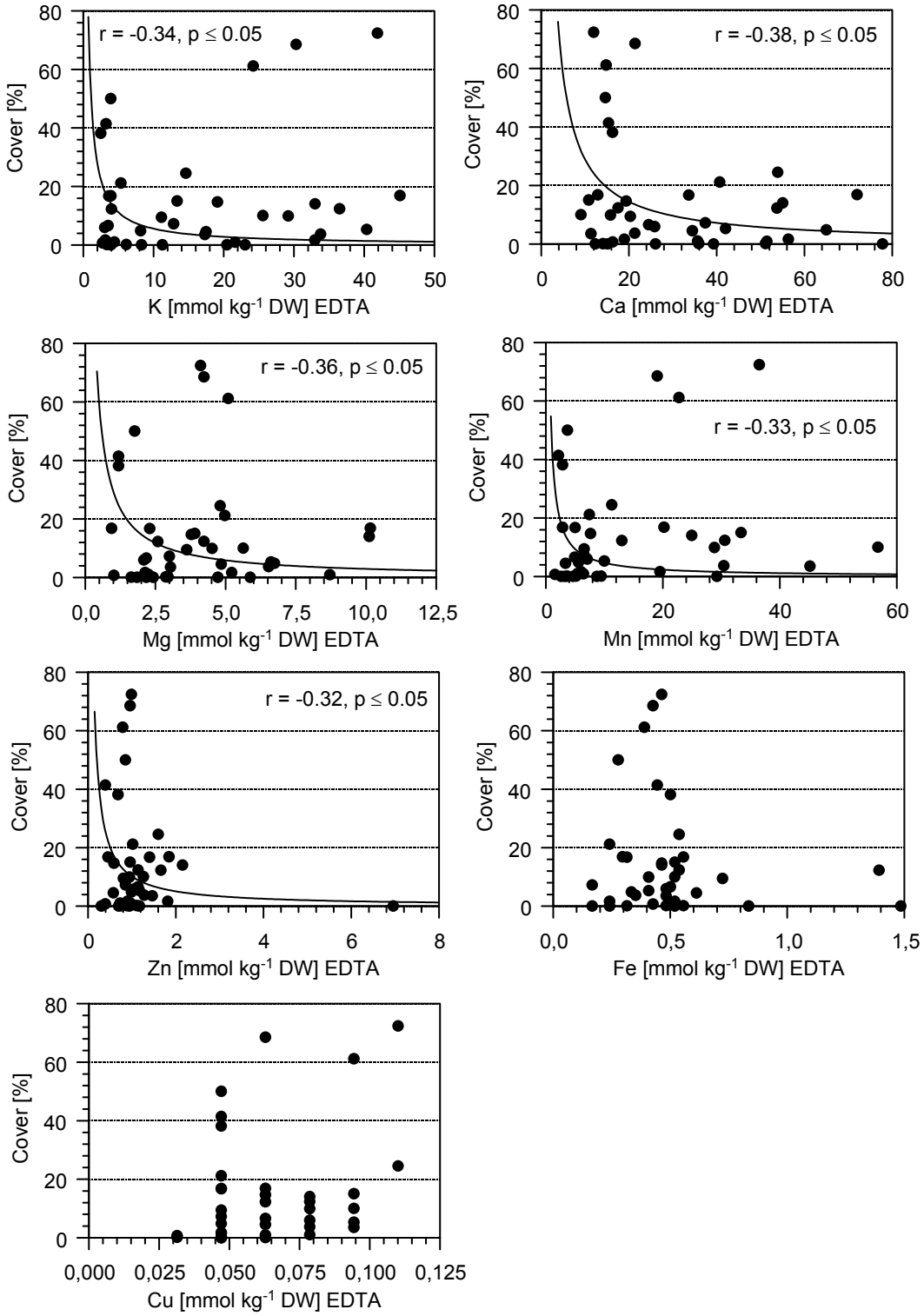

Fig. 4-21. Lichen cover of *Arthonia caesia* vs. element content of extraction with EDTA. Regression model: a/(b*x). n = 40.

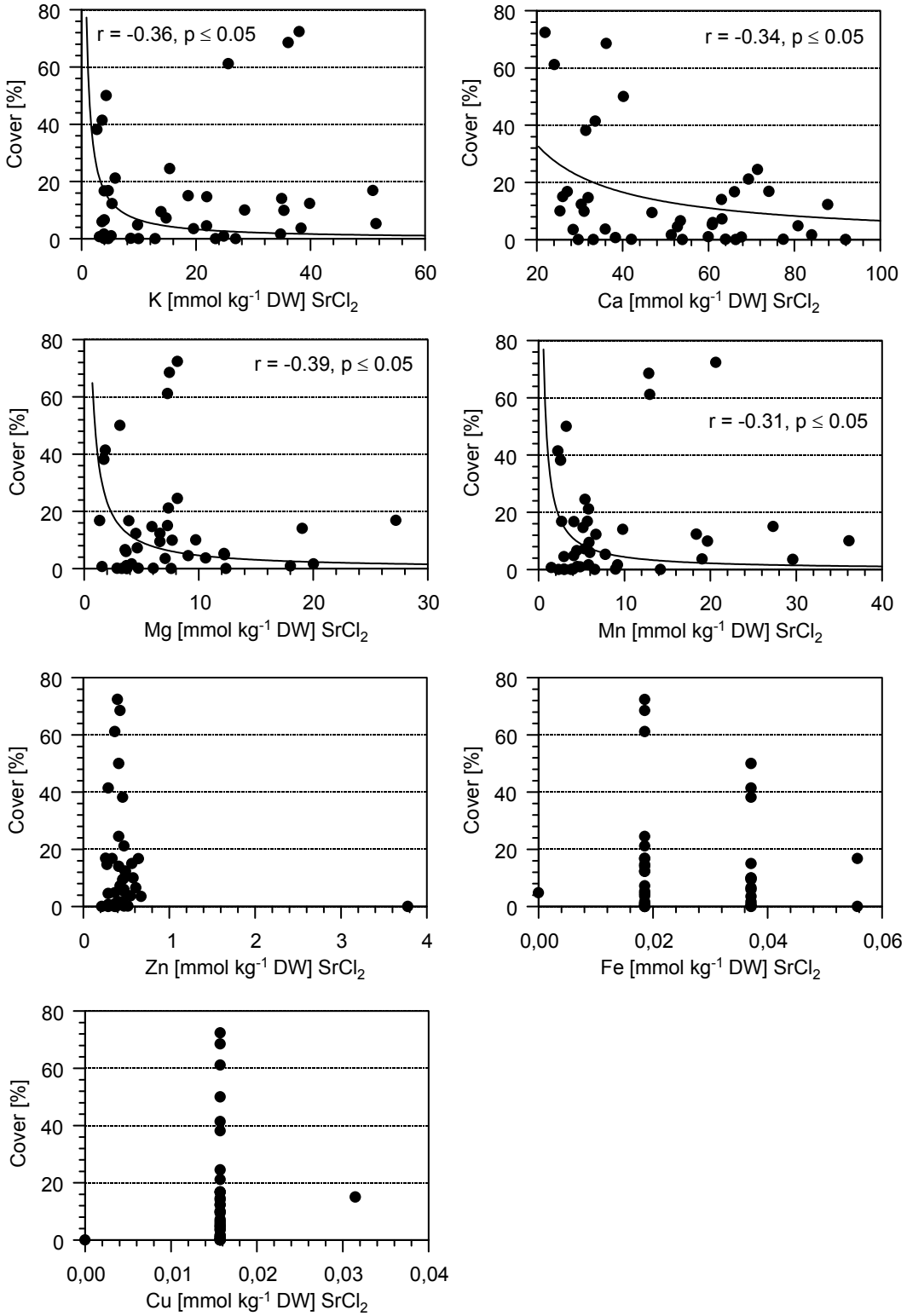

Fig. 4-22. Lichen cover of *Arthonia caesia* vs. element content of extraction with $SrCl_2$. Regression model: a/(b*x). n = 40.

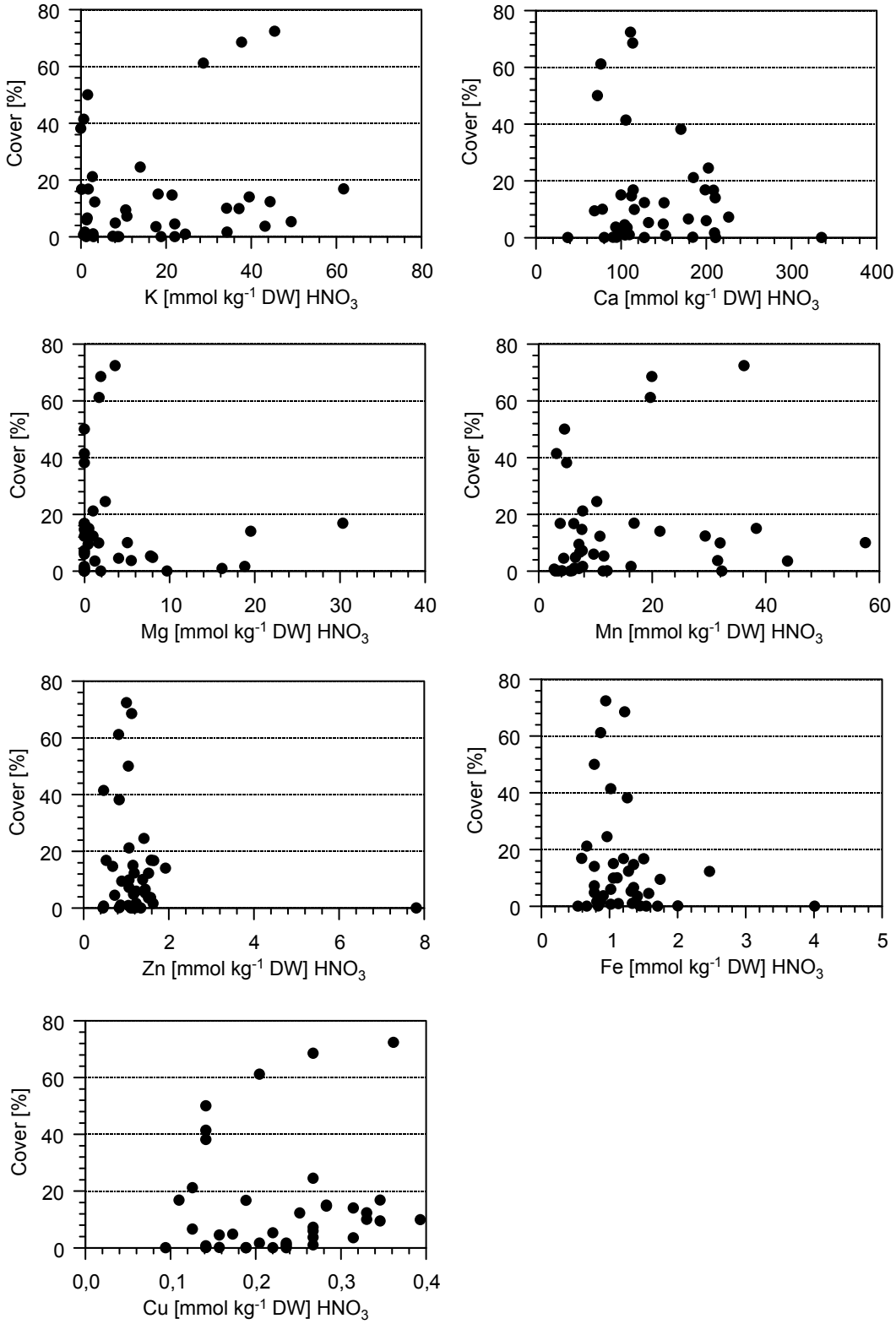

Fig. 4-23. Lichen cover of *Arthonia caesia* vs. total bark content. Regression model: a/(b*x). n = 40.

4.7.3 Microclimate

Cover of most lichen species did not correlate with microclimatic parameters. For light measurements, cover of six species increased with increasing PPFD (Tab. 4-21), whereas cover of *Arthonia caesia* and *Bryoria nadvornikiana* was significantly higher on trees with the lowest PPFD than on trees with the highest PPFD. *Evernia mesomorpha*, *Lecidea nylanderi*, and *Pseudevernia consocians* occurred with higher mean cover on trees with the highest PPFD.

Tab. 4-21. Correlation between lichen cover and lowest (min.) as well as highest (max.) mean light intensity (PPFD).

			Mean cover [%]		
	r_s	p	Min. PPFD	Max. PPFD	
Arthonia caesia	.		25.8 ± 20.9	4.03 ± 5.95	*
Bryoria capillaris	0.28	*	0.03 ± 0.08	0.21 ± 0.20	
Bryoria furcellata	0.33	**	0.03 ± 0.08	0.08 ± 0.13	
Bryoria nadvornikiana	-0.34	**	0.18 ± 0.20	0.03 ± 0.08	**
Evernia mesomorpha	0.31	*	0.00 ± 0.00	0.10 ± 0.13	*
Lecidea nylanderi	0.28	*	2.00 ± 6.32	11.0 ± 11.1	**
Pseudevernia consocians	0.36	**	0.03 ± 0.08	0.50 ± 0.58	**
Usnea spec.	0.25	*	0.13 ± 0.06	1.95 ± 1.73	

Mean cover: Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. $n = 60$. r_s: Spearman correlation coefficient. Measurements carried out for 12 days.

Loxospora ochrophaea was the only lichen relatively closely correlated with evaporation. Cover decreased with increasing evaporation (daily and hourly measurements; Tab. 4-22). Additionally, *Loxospora ochrophaea* had higher mean cover on the ten trees with lowest daily mean evaporation than on the ten trees with the highest evaporation. A similar, but weaker, correlation was found for *Bryoria nadvornikiana*. Positive correlations between lichen cover and evaporation were found for *Hypogymnia krogiae*, *Imshaugia aleurites*, and *Lecidea nylanderi*, but only *I. aleurites* occurred with significantly higher mean cover on the ten trees with highest evaporation than on the ten trees with lowest evaporation.

Tab. 4-22. Correlation between lichen cover and lowest (min.) as well as highest (max.) mean evaporation.

			Mean cover [%]		
	r_s	p	Min. evap.	Max. evap.	
Bryoria nadvornikiana	-0.32	*	0.28 ± 0.40	0.00 ± 0.00	*
Hypogymnia krogiae	0.33	*	0.69 ± 0.43	1.29 ± 0.43	
Imshaugia aleurites	0.40	**	1.35 ± 1.92	8.23 ± 9.42	*
Lecidea nylanderi	0.42	**	4.80 ± 7.90	8.73 ± 9.31	
Loxospora ochrophaea[a]	-0.47	**	18.2 ± 18.7	0.15 ± 0.47	*
Usnea spec.	.		1.03 ± 1.29	0.18 ± 0.17	*

Mean cover: Arithmetic mean ± standard deviation. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. $n = 40$. r_s: Spearman correlation coefficient. Measurements carried out for one month. [a]: Correlation between cover of *L. ochrophaea* and hourly mean evaporation: $r_s = -0.65$, $p \leq 0.05$.

Only a few correlations were found between lichen cover and other parameters, such as relative humidity (*Bryoria nadvornikiana*: $r_s = -0.58$, $p \leq 0.05$), air temperature (*Micarea prasina*: $r_s = 0.60$, $p \leq 0.05$), and water-holding capacity of bark (*Evernia mesomorpha*: $r_s = -0.30$, $p \leq 0.05$; *Pseudevernia consocians*: $r_s = -0.47$, $p \leq 0.01$).

5 Discussion

5.1 Lichen vegetation

5.1.1 Influence of tree species on epiphytic lichen vegetation

There was no difference between dead *Abies balsamea* and dead *Picea rubens* but there was between their living counterparts in A) number of lichens, B) mean cover, and C) constancy. 40 lichens grew on living *Abies balsamea*, whereas 35 occurred on living *Picea rubens*. Compared to *Picea rubens*, five crustose species occurred with a higher mean cover on *Abies balsamea*. This was also true for four foliose, three fruticose, and two pendulous ones. In contrast, *Picea rubens* was inhabited by only three crustose lichen species that had a higher mean cover than *Abies balsamea*.

Foliose and pendulous species growing on Whiteface Mountain with a higher frequency (mean cover and/or constancy) on living fir than on living spruce, such as *Hypogymnia physodes*, *Parmelia saxatilis*, *Platismatia glauca*, and *Bryoria capillaris* are species that prefer habitats with high light intensities. They are low to moderately nitrophytic, and moderately to strong acidophytic (WIRTH 1995). In Germany, *Hypogymnia physodes* grows with *Pseudevernia furfuracea* and *Platismatia glauca* in bulk densities (WIRTH 1995). The *Pseudevernia* species found on Whiteface Mountain differ in their chemistry compared to *Pseudevernia furfuracea* (HALE 1968), but through observations made in the field it can be assumed that they have a similar ecology. The crustose lichens with a higher mean cover on spruce were *Haematomma ochroleucum*, *Japewia subaurifera*, *Loxospora cismonica*, *Mycoblastus sanguinarius*, and *Ropalospora chlorantha*. In ecological descriptions previously published (for all species, except for *Ropalospora chlorantha*), lichen species are described as either growing on acidic bark (*Japewia subaurifera*; TØNSBERG 1990) or being moderately to strong acidophytic (*Haematomma ochroleucum*, *Loxospora cismonica*, *Mycoblastus sanguinarius*; WIRTH 1995). *Haematomma ochroleucum* and *Loxospora cismonica* grow preferentially on *Abies* (WIRTH 1995).

The crustose lichens with a higher mean cover on living spruce compared to living fir were *Hypocenomyce friesii*, *H. scalaris*, and *Mycoblastus fucatus*. *Hypocenomyce scalaris* is known for its toxitolerance (KAUPPI & HALONEN 1992), and is probably, as *Mycoblastus fucatus*, promoted by the anthropogenic increase of acidic bark substrates (WIRTH 1995). *Hypocenomyce friesii* is known for its preference for moderately to highly acidic bark (WIRTH 1995). Additionally, *Hypocenomyce scalaris* was a species restricted to spruce at the field site on Whiteface Mountain.

Generally, crustose lichens tend to be more toxitolerant than foliose and fruticose ones (WIRTH & TÜRK 1975), because only the upper surface of the crustose thallus is exposed to the atmosphere. Fruticose lichens with a much greater surface area related to their volume than other growth forms can accumulate more (toxic) substances and thus, are more sensitive to damage (RICHARDSON 1988).

The phenomenon of more lichen species on *Abies* than on *Picea* is an observation made by researchers in the U.S.A. as well as in Central Europe. In a spruce-fir forest of British Columbia, CAMPBELL & COXSON (2001) recorded a higher biomass of the pendulous lichen genera *Alectoria* and *Bryoria* as well as of foliose lichens on *Abies lasiocarpa* than on *Picea engelmannii*. LANG et al. (1980) found in forests, similar to those on Whiteface Mountain, a rich epiphytic lichen vegetation on *Abies balsamea* in New Hampshire, but did not compare it with the vegetation on *Picea rubens*. In forests of Germany, GLIEMEROTH (1990) found a more diverse lichen vegetation of particularly pendulous lichens on *Abies alba* than on *Picea abies*. In a mixed forest of spruce, fir, maple, and beech in the Austrian Alps, PFEFFERKORN (1996) found twice as many epiphytic lichens on *Abies alba* than on *Picea abies*. In a study with six different tree species (conifers as well as deciduous trees, but without the genus *Abies*) in Finland, KUUSINEN (1996) found out that compared to all other tree species, *Picea abies* was inhabited by the lowest average species number per tree.

5.1.2 Influence of tree vitality on epiphytic lichen vegetation

A higher number of lichen species as well as higher mean cover and a higher constancy were found on dead than on living trees. This was especially true for *Picea rubens*, but applied also (except for constancy) to a lesser extent to *Abies balsamea*.

Three foliose, seven fruticose, two pendulous, and three crustose lichen species had a higher mean cover on dead *Picea* than on living ones.

Only *Lecidea nylanderi* occurred with a higher mean cover on living than on dead spruce. *Lecidea nylanderi* is known to be strongly acidophytic and non-nitrophytic. When constancy was taken into account, two additional species (*Imshaugia aleurites*, *Parmeliopsis capitata*) occurred with a higher frequency on living as compared to dead *Picea*. Compared to *Platismatia glauca* and *Bryoria capillaris*, two species more frequent on dead *Picea* on Whiteface Mountain, *Imshaugia aleurites* and *Parmeliopsis capitata* are more resistant to pollution (KAUPPI & HALONEN 1992).

Two species with a higher frequency on dead than on living spruce were *Micarea prasina* and *Cladonia coniocraea*. *Micarea prasina* prefers acid, shady and humid habitats with low competitive pressure and has a preference for wood and bark. The latter preference applies also to *Cladonia coniocraea*. However, *Cladonia coniocraea* is rather indifferent to light and humidity and has a greater competitive capacity than the *Micarea* species (CARLIN 1981, WIRTH 1995). In general *Cladonia* species tolerate higher levels of pollution as compared to other fruticose lichen genera (FOLKESON & ANDERSSON-BRINGMARK 1988, WIRTH 1992, GNÜCHTEL 1997). BRODO (1966) established *Cladonia coniocraea* to be the most toxitolerant epiphyte on Long Island, New York.

BASTIEN et al. (1998) found, as in the present work, an increasing diversity of epiphytic lichens along with decreasing vitality of *Acer saccharum* in dieback-affected stands of Québec. In northern Sweden, several *Cladonia* species and calicioid lichens were characterized as typical lichens of dead (of natural mortality) spruce trees (KRUYS et al. 1999). This is in accordance with five

Cladonia and one *Chaenotheca* species that were more frequent on dead spruce than on living ones on Whiteface Mountain.

The difference in lichen growth was not as obvious between dead and living *Abies balsamea* as between dead and living *Picea rubens*. This is in accordance with investigations carried out by ARSENAU et al. (1998) in an old-growth balsam fir forest in Québec.

Only one foliose (*Parmelia saxatilis*) and two fruticose (*Cladonia coniocraea*, *C. fimbriata*) lichen species as well as two crustose ones (*Loxospora ochrophaea*, *Ropalospora chlorantha*) occurred with higher mean cover on dead than on living fir. There is not much published about the ecology and/or pollution-sensitivity of *Loxospora ochrophaea* and *Ropalospora chlorantha*, except that the former grows on conifers (BRODO 2001) and the latter can be found on the bark of a variety of deciduous and coniferous trees (BRODO 2001).

Species, more frequent on living than on dead fir were *Imshaugia aleurites* (foliose lichen) as well as *Arthonia caesia* and *Loxospora cismonica* (crustose lichens). *Arthonia caesia* is a moderately acidophytic species that mostly inhabits bark (WIRTH 1995, BRODO 2001). When only constancy was taken into account, four additional species were more frequent on living than on dead fir: *Japewia subaurifera*, *Lecanora impudens*, *Mycoblastus sanguinarius* (crustose lichens), and *Platismatia glauca* (foliose lichen). *Lecanora impudens* grows on cracked, up to moderately acidic bark and grows preferentially on the genus *Fraxinus* (WIRTH 1995).

More pollution-sensitive species occurred on dead trees of each species as compared to their living counterparts. Additionally, a higher total lichen diversity and a higher diversity within the pollution-sensitive lichen growth forms (foliose, fruticose, and pendulous) was found per tree on dead than on living *Picea* (Tab. 5-1). Again, for dead and living *Abies* the difference was not significant.

Tab. 5-1. Total of lichen species per sample tree.

	R	DR	B	DB
Total	9.8 ± 4.9 a	14.1 ± 6.1 b	14.2 ± 4.9 b	14.8 ± 6.1 b
Crustose	4.3 ± 1.2 a	4.5 ± 1.5 a	5.3 ± 1.2 b	5.2 ± 1.2 b
Foliose	3.1 ± 0.9 a	3.8 ± 0.9 bd	4.3 ± 0.8 cd	4.1 ± 1.0 d
Fruticose	1.2 ± 1.0 a	3.5 ± 1.5 b	2.2 ± 1.0 c	3.1 ± 1.2 b
Pendulous	1.2 ± 1.1 a	2.2 ± 1.3 b	2.4 ± 1.4 b	2.4 ± 1.5 b
Absolute total	35 a	40 a	39 a	38 a

Arithmetic means ± standard deviation. Statistics: U-test; last row: χ^2-test; $p \leq 0.05$; Within a row, means sharing a common letter do not differ significantly.

An increased lichen diversity in damaged montane coniferous forests was also observed in Germany. HAUCK (2000) found a higher lichen diversity on *Picea abies* trunks at a height of 100 – 200 cm above ground in a dieback affected stand as compared to a healthy stand in the Harz Mountains. He also remarked that pollution-sensitive species were more frequent in the former than in the latter. On *Abies alba* and *Picea abies* in the Black Forest in Southern Germany, GLIEMEROTH recorded in 1990 and 1993 an increase in pollution-sensitive lichen species with an increasing damage of the forest. The relevés were taken from

trunks at a height of 50 – 200 cm above the ground and the vegetation was mapped by recording the presence of selected lichen species. BARTHOLMESS (1989) and STORM (1996), both carrying out studies in the Black Forest, found similar results: The former established in a stand of *Abies alba* a positive correlation between needle loss and the occurrence of *Hypogymnia physodes* and *Pseudevernia furfuracea*, whereas the latter noticed increasing cover values of *Bryoria* and *Usnea* in an affected stand of *Picea abies*. MACHER & STEUBING (1984, 1986) and STEUBING & MACHER (1985) found several pollution-sensitive lichen species (e.g. *Alectoria sarmentosa*, *Bryoria capillaris*, *B. fuscescens*, *Evernia divaricata*, *Hypogymnia vittata* as well as several *Usnea* species) in a stand of *Picea abies* in the Bavarian Forest, but found the lichen vegetation negatively influenced by forest dieback. However, MACHER & STEUBING (1984, 1986) only included trees with intact bark in their study, whereas dead trees with decaying bark are known to bear a particularly rich lichen vegetation (KRUYS et al. 1999, HAUCK 2000). The highest average number of species was also found by JOHANSSON (1997) on living spruce, and lowest on decaying logs in a lowland *Picea abies* and *Pinus sylvestris* stand in Gotland, Sweden.

Lichen cover increased in four out of five cases (*Arthonia caesia*, *Hypogymnia physodes*, *Imshaugia aleurites*, and *Lecidea nylanderi*) on *Picea rubens* and in three out of five cases (*Hypogymnia physodes*, *Imshaugia aleurites*, and *Lepraria jackii*) on *Abies balsamea* from vitality class V to IV. Class II showed the lowest lichen cover in most of the cases, whereas from vitality class II to I lichen cover mostly increased. A change of lichen cover with increasing bark decay was also observed by CRITES & DALE (1998). They found in an aspen mixedwood boreal forest in Canada a lower nonvasuclar species richness in decay stages 1 and 2 (log whole and undecayed, bark, branches, and twigs present and intact, log elevated on support points; log sound, wood hard, twigs mostly lacking, less than 50 % of the bark missing), but an increasing and higher remaining richness in decay stages 3 to 7 (wood soft in places, some branches remaining, 50 % or more of the bark missing; humification nearly 100 %, hard to define as a log, no evidence of hard wood). They concluded that downed wood in different stages of decay are important to maintaining assemblages of bryophytes, lichens, and fungi.

The unequal number of trees grouped into the five vitality classes I to V was due to random selection of trees; a method necessary for comparing the epiphyte vegetation and bark chemistry between the two tree species and their variants dead and healthy. As nearly two thirds of the living trees of both species belonged to vitality class V, classes IV to II were underrepresented.

Apart from differences in frequencies, different degrees of variation of cover values distinguished living *Abies balsamea* from living *Picea rubens* as well as dead from living *Picea rubens*, the two pairwise comparisons showing the highest difference in lichen growth. Approximately twice as many lichen species occurred with a larger range of cover values on living *Abies* than on living *Picea* and on dead than on living *Picea*, respectively. The larger range corresponded to higher maximum cover values on the respective tree. More lichen species were inhabited on living *Abies balsamea* and on dead *Picea rubens* compared to living *Picea rubens*. This leads to the conclusion that epiphyte vegetation was less uniform on living *Abies* and on dead *Picea* than on living *Picea*. Thus, if one selected randomly an infinitesimally small point of bark surface, the probability of

hitting a certain species was significantly lower on living *Abies* and dead *Picea* as compared to living *Picea*. Differences in the degree of variation between dead and living *Abies balsamea* as well as dead *Abies balsamea* and dead *Picea rubens* were small.

5.2 Element deposition

5.2.1 Incident precipitation

An influence of incident precipitation on differences in element content of stem flow and bark on the field site of Whiteface Mountain can be ruled out, as only one 100 x 100 m plot of equal exposition and inclination was studied. Within this stand variation of incident precipitation is not very likely as precipitation did not differ between the two sample stations at 1000 and 1200 m elevation.

The results are in accordance with chemical analyses of incident precipitation, carried out at an elevation of 610 m on the northeastern slope of Whiteface Mountain (National Atmospheric Deposition Program, station NY98; 44°23'36'' N, 73°51'34'' W; Tab. 5-2) with respect to Ca and Mg concentrations, pH, conductivity, and the amount. Concentrations of NH_4^+, K, and Na were higher in precipitation at the field site, whereas the concentrations of NO_3^- and SO_4^{2-}-S were higher at the station at 610 m. The deficit of anions is covered by the amount of Cl^- ions (Tab. 5-2). For the field site, Cl^- was not determined.

Differences in concentration between field site and station NY98 are due to distinctions in elevation and exposition of the two sample localities and thus, to different weather conditions. In contrast to the two stations at the field site (elevation of 1000 and 1200 m), the station NY98 on Whiteface Mountain is located on much lower altitude. It is known that element concentrations (cations as well as anions) are much higher in mist events (i.e. cloudwater; approximately one dimension) than in incident precipitation (CONSTANTIN 1993). As clouds extend as low as 1000 m for 15 % of the year (MOHNEN 1989), a higher element input might occur at times at the field site. Additionally, the position of the samplers are of importance. Samplers of the field site were located near the Whiteface Mountain toll road at the northwestern slope of Mt. Esther, while the one at the station was standing on grassland at the northeastern slope of Whiteface Mountain. The wind direction is mainly westwards. Thus, different rates of wet and dry deposition due to dust immission from the road and/or due to differences in element load resulting from the main wind direction are most likely to expect.

Tab. 5-2. Element concentrations and amount of incident precipitation for 1999 and 2000 at the field site in comparison with measurements from the National Atmospheric Deposition Program from Whiteface Mountain.

	1999		2000	
	Field site	Station NY98	Field site	Station NY98
NH_4^+ [µmol l^{-1}]	62.1 ± 46.5	12.1 ± 8.00	67.0 ± 35.7	11.9 ± 8.91
NO_3^- [µmol l^{-1}]	4.01 ± 4.20	18.2 ± 9.76	2.49 ± 2.74	17.9 ± 11.4
SO_4^{2-}-S [µmol l^{-1}]	2.51 ± 1.53	16.3 ± 10.4	2.11 ± 1.25	19.6 ± 19.1
K [µmol l^{-1}]	16.5 ± 10.3	0.23 ± 0.16	11.8 ± 16.5	0.34 ± 0.37
Na [µmol l^{-1}]	18.8 ± 4.80	1.17 ± 1.92	16.7 ± 2.77	0.73 ± 0.87
Ca [µmol l^{-1}]	3.16 ± 3.20	2.09 ± 1.24	4.23 ± 1.20	1.89 ± 1.61
Mg [µmol l^{-1}]	0.69 ± 1.17	0.52 ± 0.35	0.39 ± 0.40	0.45 ± 0.39
Cl [µmol l^{-1}]	-	1.89 ± 1.27	-	1.66 ± 1.38
pH	4.41 ± 0.21	4.60 ± 0.35	4.39 ± 0.17	4.55 ± 0.32
Conductivity [µS cm^{-2}]	20.8 ± 10.6	18.4 ± 10.4	21.1 ± 8.68	20.6 ± 17.7
Precipitation [mm $week^{-1}$]	36.5 ± 31.9	30.8 ± 35.3	28.4 ± 8.90	22.2 ± 9.64

Arithmetic mean ± standard deviation. n: field site = 6, Station NY98 = 1. Measuring periods: June – September; 15 weeks in 1999 for field site and 14 weeks for station NY98, 16 weeks in 2000; weekly measurements.

A comparison of incident precipitation data from the Harz Mountains, Germany (HAUCK 2000) with data from the field site on Whiteface Mountain revealed lower NO_3^- and S concentrations in samples of the latter locality (Tab. 5-3).

Tab. 5-3. NO_3^- and S concentrations [µmol l^{-1}] and pH of incident precipitation in samples from the Harz Mountains, Germany, and Whiteface Mountain, U.S.A.

	Year[a]	Harz Mountains		Whiteface Mountain
		F1[b]	W1[c]	FS[d]
NO_3^-	1	44.5 ± 33.8	51.0 ± 32.6	4.01 ± 4.20
	2	90.0 ± 33.1	85.3 ± 32.9	2.49 ± 2.74
S	1	64.3 ± 30.6	82.2 ± 44.8	2.51 ± 1.53
	2	39.1 ± 39.7	36.1 ± 37.5	2.11 ± 1.25
pH	1	4.63 ± 0.31	4.82 ± 0.58	4.41 ± 0.21
	2	3.95 ± 0.28	3.92 ± 0.27	4.39 ± 0.17

Arithmetic mean ± standard deviation. [a]: Year of measurements: Harz Mountains: 1 = 1995, 2 = 1997/1998; Whiteface Mountain: 1 = 1999, 2 = 2000. [b]: Healthy selectively-harvested forest, [c]: Dieback-affected stand, [d]: Field site on Whiteface Mountain.

5.2.2 Causes of tree mortality of *Abies balsamea* and *Picea rubens*

Studies in the southern Appalachian Mountains and on Whiteface Mountain showed that in high elevation sites (> 1100 m) *Picea rubens* is affected by air pollutants. Acidic cloudwater reduces the freezing resistance of the spruce trees and accelerates foliar loss to the point where the trees are unable to adequately replace the lost foliage because of reduced photosynthetic capacity (THORNTON et al. 1993, EAMUS 1993, JOHNSON 1992, VANN et al. 1992, SHEPPARD 1994). S deposition was determined to be the main cause for spruce decline (JOHNSON 1992, LEITH et al. 1995) by protein denaturation and the loss of membrane integrity (SHEPPARD 1994), whereas ozone showed no significant influence (THORNTON et al. 1993, VANN et al. 1992, SAYRE & FAHEY 1999). During the discussion which factor caused the decline of *Picea rubens* in the U.S.A., the S deposition was much higher than the deposition nowadays. Even in the mid to late 1980s (1984 – 1989) the measured S concentrations on Whiteface Mountain were higher compared to those of the years 1995 – 2000: 20.1 µmol l^{-1} vs. 12.1 µmol l^{-1} (National Atmospheric Deposition Program, station NY98; 44°23'36'' N, 73°51'34'' W). Treatments with NO_3^- alleviated the toxic effect of S (SHEPPARD et al. 1993, LEITH et al. 1995). This was attributed to consumption of SO_4^{2-} ions in assimilation processes (SHEPPARD 1994). *Abies balsamea*, in contrast to *Picea rubens*, remains unaffected by pollutant-caused forest decline. This implies that balsam fir is not as sensitive to S-immission as red spruce is. Remarkably, a reverse observation of pollution-sensitivity between the genera *Abies* and *Picea* can be made in Central Europe: *Abies alba* is highly affected by forest dieback, whereas *Picea abies* seems more resistant. A study of SO_4^{2-} accumulation rates of different gymnosperm species showed that needles of the most sensitive species (*Picea abies*) accumulated more SO_4^{2-} than needles of *Picea pungens*, *Pinus mugo*, and *P. sylvestris* (SLOVIK et al. 1995). Furthermore, *Abies balsamea* has been found to have less efficiency in fog collection as compared to *Picea rubens* and *P. abies* (JAGELS 1991).

5.2.3 Significance of stem flow for the water balance of the forest ecosystem

The impact of stem flow on the hydrological balance of the entire forest ecosystem is negligible, as shown in *Picea abies* stands (DELFS et al. 1958, BENECKE 1984, HAUCK 2000). Only 0.1 – 0.2 % (HAUCK 2000) to 0.8 % (DELFS et al. 1958) of the incident precipitation reached the forest floor as stem flow. NIHLGÅRD (1970) reported that stem flow was as high as 3 % of incident rainfall in a *Picea abies* forest. The low significance of stem flow for the water balance of spruce forests is due to the morphology of the tree crowns (MÜLLER 1981, SCHMIDT-VOGT 1986). Throughfall instead, is much higher; NIHLGÅRD (1970) calculated an average value of 58 %. In comparison, the estimated value for a beech forest was 70 %. HANSEN (1995) was able to show in his experiment with *Picea abies*, that with increasing distance from the trunk throughfall increases. The highest quantity of throughfall could be measured at the top of the tree which decreased down through the canopy, whereas approximately

50 % of the precipitation was collected beneath the canopy. In an 80-year-old stand investigated by DELFS et al. (1958), 63 % of the precipitation reached the forest floor as throughfall, while BENECKE (1984) determined 60 – 80 % for throughfall. Due to the fine structure of the needles, which develop a net-like structure, impaction and diffusion deposition gets promoted (CONSTANTIN 1993). NIHLGÅRD (1970) calculated an interception of 39 % for a spruce forest, while the interception of a beech forest was estimated with only 19 %. Especially in mist events (mostly cloudwater), which are frequently observed on Whiteface Mountain, droplets are deposited on the needles due to their size and complete adhesive strength (CONSTANTIN 1993, DELFS et al. 1958). In years or rain events with little incident precipitation, interception of the trees is higher than in years or rain events with high precipitation (DELFS et al. 1958).

In addition to leaf structure, bark structure plays an important role for the amount of stem flow reaching the forest floor. Trees with rough bark and tall trunks need more rain until stem flow occurs, as the amount which is necessary to wet the surface of the trunk is higher (DELFS et al. 1958).

In stands of *Fagus sylvatica*, stem flow is more important, as 4 –7 % of incident precipitation reach the forest floor as stem flow (BENECKE, 1984, GERKE 1987, LEUSCHNER 1994). This is due to the crown structure of *Fagus sylvatica*: The lower the angle of the branche's attachment compared to the trunk, the more water is collected in the canopy and reaches the forest floor as stem flow (DELFS et al. 1958).

Despite the low importance of the stem flow for the water balance in coniferous forests on the ecosystem level, stem flow is, in addition air humidity, the main water source for epiphytes.

5.2.4 Element deposition and its modification in the canopy

Element deposition from the atmosphere on the canopy of trees takes place as dry and wet deposition. Wet deposition occurs as rain, fog, hale or snow (SCHMIDT 1987) and it can be distinguished between:

(a) Rainout, occurring in clouds. Due to condensation water vapor accumulates on aerosols; also gases can get absorbed by additional accumulation.
(b) Washout, occurring below cloud cover. Through falling raindrops additional particles (mainly aerosols with a radius > 1 µm) can get absorbed.

Dry deposition is sedimentation of particles during precipitation free periods (SCHMIDT 1987).

Element concentration of wet deposition (i.e. incident precipitation) can be modified in the canopy by the following processes (SCHMIDT 1987):

(1) Wash-out of dry deposition,
(2) leaching,
(3) evaporation,
(4) adsorption and assimilation.

The last process decreases the element concentration in throughfall and in stem flow, whereas the first three increase the element content. The net result of these

processes determines the availability of ions for intrasystem elemental cycling (LANG et al. 1976).

The enrichment of incident precipitation on the way through the canopy with substances was established in numerous ecosystem studies (e.g. CARLISE et al. 1967, MATZNER 1988, LINDROOS et al. 1998).

K, Mn and Zn are according to NIHLGÅRD (1970), FASSBENDER (1977), and SCHMIDT (1987) mainly leachates from the canopy and thus plant originated, whereas Na, Mg, Ca, and Cl are primarily derived from atmospheric interception (GODT 1986). A spruce forest in southern Sweden absorbed the same amount of aerosols as a beech forest (NIHLGÅRD 1970). Higher amounts of nutrients in the throughfall of the spruce forest probably derived from higher leaching in the canopy. Leaching rates of heavy metals other than Mn and Zn or of Na are negligible (GODT 1986). The significance of leaching in modifying the amounts of Ca and Mg is controversial (FASSBENDER 1977, GODT 1986, BREDEMEIER 1987, MATZNER 1988, SAYRE & FAHEY 1999).

MATZNER (1988) mentions the deposition of Mn as negligible in the Solling, Germany, whereas Mn and Zn are recognized as important heavy metal pollutants in the air by NRIAGU (1990). Since the 1970s Mn is used instead of Pb in gasoline in Canada and is released in its toxic oxidized forms in the atmosphere from car exhaust (LORANGER & ZAYED 1994). In spruce forests of eastern North America, PETTY & LINDBERG (1990) reported leaching of Mn from interior needle tissues and uptake of Zn by foliar surfaces. Results of LIN et al. (1996 a) indicated that the isotope ^{54}Mn is more mobile than the isotope ^{65}Zn in balsam fir seedlings, with both Mn and Zn are usually classified as intermediate in terms of element mobility (KRAMER & KOZLOWSKI 1979). Migration of ^{54}Mn and ^{65}Zn from internal tissues to epicuticular wax layers only accounted for 0.002 to 0.01 % for ^{54}Mn and 0.124 to 0.541 % for ^{65} Zn of the total radioactivities in shoots (LIN et al. 1996 a). This might suggest that root uptake and consequent translocation of Mn and Zn to shoots would not result in a significant contribution of these elements to the throughfall/foliar rinsing composition through physiological ion migration from internal tissues to epicuticular wax layers (LIN et al. 1996 a). Overall, leaching ratios were well below 0.5 % for Mn and 1.0 % for Zn (LIN et al. 1996 a).

Airborne Zn, originated from tire wear, fuel emissions, and brake linings in large industrial-metropolitan areas is one of the major sources of atmospheric Zn pollution (LIN et al. 1995). Dry deposition of Mn and Zn from the atmosphere to forest surfaces is usually estimated from throughfall measurements or foliar rinsing (LINDBERG & LOVETT 1985, PETTY & LINDBERG 1990). Although controlled experiments showed negligible migration of ions from internal tissues to needle surfaces during dry deposition periods (REINERS et al. 1986), leaching of metal elements in acid rain may contribute significantly to the estimate of dry deposition (LINDBERG & GARTEN 1988). SCHMIDT (1987) concluded that approximately one fifth of Zn and Cd deposited in the canopy are plant originated. Zn, Pb, Cd, and with restriction Cu are equally deposited as wet and dry deposition (SCHMIDT 1987).

N can be deposited, similar to S, as gaseous deposition (NH_3, NO_x, HNO_3-vapor) or as particles (MATZNER 1988, BOYCE et al.1996). Within the crown area NO_3^- can be reduced to NH_4^+ from microorganisms and by the tree itself, whereby NH_4^+ can be further assimilated to amino acids, or conversions between the

different N forms NH_4^+, NO_3^-, N_{org}, NO_x, N_2, and NH_3 can take place. While branch assimilation from *Picea rubens* growing on Whiteface Mountain is about 5 % of NH_4^+ and 1 % of NO_3^-, canopy assimilation rates are expected to be 3 - 6 times larger (BOYCE et al. 1996). Areas unaffected by air pollution typically have N deposition rates of 2 – 5 kg N ha^{-1} yr^{-1} (JOHNSON et al. 1982, LOVETT 1992). High-elevation red spruce-balsam fir forests in the northeastern U.S.A. receive approximately 16 – 30 kg N ha^{-1} yr^{-1} in the form of precipitation, cloudwater, and dry deposition (FRIEDLAND et al. 1991, MILLER et al. 1993). LANG et al. (1976), investigating N uptake in the crown area of balsam fir, discovered a temperature-dependent maximum in the summer. SAYRE & FAHEY (1999) observed a retention of both NO_3^- and SO_4^{2-} in the canopy of *Picea rubens*.

SO_2 is only one of several S compounds present in the atmosphere, but vegetation is a substantial scavenger of SO_2. Other important forms are H_2SO_4 or SO_4^{2-}. 'Primary' SO_2 is emitted almost entirely from pollution sources (ROBINSON & ROBINS 1970), whereas 'secondary' SO_2 is formed by oxidation of H_2SO_4 derived mainly from natural processes (SAUNDERS & WOOD 1973). S can be removed from the atmosphere by wet and dry deposition, whereby the latter may account for about 80 % of atmospheric SO_2 (MEETHAM 1950, CHAMBERLAIN 1960, JUNGE 1963, SPEDDING 1969). SAUNDERS & WOOD (1973) calculated that approximately 12 % of atmospheric S arrives on plant surfaces as SO_2. S is the element for which interception deposition most strongly influences stem flow in Germany. GODT (1986) reported an interception deposition of S that was 3 – 6 times the amount deposited by incident precipitation in a forest with *Picea abies*. Gaseous SO_2 does not show up completely in stem flow and throughfall, as studies of SLOVIK et al. (1995) and VEITHEN (1996) showed, as it is partly absorbed by the needles of *Picea abies* and other parts of the plant (SAUNDERS & WOOD 1973). The basic reactions of SO_2 under conditions of high humidity or surface moisture are accelerated, producing less toxic SO_4^{2-} and indirectly rising the pH (SAUNDERS & WOOD 1973).

5.2.5 The role of epiphytic lichens in altering element composition of precipitation

Not only higher plants, but also epiphytic lichens can play an important role in biogeochemical processes and in the change of nutrient cycling in forests underneath the canopy by either enriching or decreasing the concentrations of the throughfall (LANG et al. 1976, NIEBOER et al. 1978, KNOPS et al. 1996). This applies to ecosystems where they contribute a substantial amount of biomass to the canopy (BOUCHER & NASH 1990). Particulate trapping of dust particles as well as air pollutant aerosols is a well-demonstrated fact in lichens (NIEBOER et al. 1978, GARTY et al. 1979, NIEBOER & RICHARDSON 1981, PUCKETT 1988, BOONPRAGOOB & NASH 1990). LANG et al. (1976) were able to demonstrate that Ca and Mg concentrations increased in incubation media of *Platismatia glauca* with increasing time. According to the authors this contributes to net ion loss from the lichen. In a stand of *Quercus douglasii* abundantly loaded with *Ramalina menziesii*, KNOPS et al. (1996) measured a higher deposition of Na, Ca, Mg, Cl, and organic N under trees with lichen cover compared to trees where

epiphytes were removed for the experiment. K, P, NO_3^-, and NH_4^+ on the other hand were not affected. While NH_4^+ was constantly absorbed by *Platismatia glauca* in the experiments of LANG et al. (1976), concentration of K first increased and then decreased in the incubation medium. The increase and later decrease was attributed to rewetting of the lichen thallus, as lichens were put into the solution in air dried conditions. K leakage is a regular feature of lichens under drying and rewetting conditions (BUCK & BROWN 1979). Foliose lichens (*Platismatia glauca*, *Hypogymnia* spp., and *Parmelia saxatilis*) absorbed more NH_4^+ than fruticose species (*Usnea* spec., *Evernia mesomorpha*, *Pseudevernia cladonia*) in the study of LANG et al. (1976). Net ion uptake of NO_3^- was compared to NH_4^+ 50 % lower (LANG et al. 1976). Behavior of dead and living lichens was different; while living lichens removed 0.81 µmol g^{-1} NH_4^+ from the water, dead lichens increased the NH_4^+ concentration of the medium by 0.49 µmol g^{-1} (LANG et al. 1976).

Accounting for the uptake of nutrients by epiphytes KNOPS et al. (1996) calculated that canopy lichens enhance the receipt of N and P from the atmosphere by 2.85 and 0.15 kg h^{-1} yr^{-1}, respectively. Further, N input in a forest ecosystem can be enhanced significantly by N_2-fixing cyanolichens (MILLBANK 1981). In a stand of *Pseudotsuga menziesii* where trees were covered with *Lobaria oregana*, DENISON (1973) estimated the participation of the lichen in total N input to be 50 %. But on the field site of Whiteface Mountain only lichens with green photobionts occurred, perhaps due to the high pollution-sensitivity of cyanolichens.

According to SAUNDERS & WOOD (1973), gaseous SO_2 is capable of penetrating the lichen thallus directly. Lichens could absorb SO_2 and its derivatives directly through their surfaces in gaseous and liquid form and indirectly via their substrates; whereby the latter possibility is suggested to be more likely (SAUNDERS & WOOD 1973). Sorption of atmospheric SO_2 into the water on the external surfaces of substrates may be a prerequisite for toxic activity (SAUNDERS & WOOD 1973). The activity of SO_2 in solution is particularly important in the failure of some lichens to establish themselves in polluted areas (GILBERT 1970, SAUNDERS 1970).

LANG et al. (1976) hypothesized the participation of three mechanisms for the release of cations from the lichen: First, the amount of intercepted aerosols present on the thallus is part of the solution enrichment. Second, ion exchange on surface sites could contribute to increased cation concentrations. Third, loss of ions from the cytoplasm would also increase the final cation concentration of that ion in solution. The latter process depends on the internal state of the organism in relation to the external environment and may be the reason for the continued and prolonged Ca and Mg losses.

In a comparison of fir needles and lichens the response was always less for needles based on their dry weight than for lichens, probably due to the thick leaf cuticle and epidermis (LANG et al. 1976). Therefore, it is not surprising that fir needles have less impact on the chemical status of solutions in submergence experiments.

5.2.6 Relations between element content of stem flow, bark, soil, and gaseous deposition

Generally gases, aerosols, fog, stem flow, and bark chemistry are the components that are relevant for the microsite of an epiphyte, and they interact in various ways with one another (HAUCK 2000). Stem flow as well as fog events contribute to the leaching process of the bark. FARMER et al. (1991) concluded from results of a study with *Quercus petraea* that the acidity of the stem flow depends on that of the bulk precipitation and on the cation status of the bark. The bark itself has the ability to buffer the acidity of stem flow, but the degree depends upon the initial cation status and is species dependent. LEGRAND et al. (1996) found an increasing pH and conductivity gradient over the trunk length of Norway spruce and silver fir, while the bark thickness decreased towards the top of the trunk of both tree species. Correlations between acidity, conductivity, bark thickness, and height could be observed especially in the upper part of the trees, whereas in the lower part spruce and fir showed the opposite behavior. In fir, pH was linked with bark thickness and distance from the ground, while conductivity was not correlated with these criteria. In contrast, it appeared on spruce that conductivity measured on the external part of bark is directly influenced by the proximity of internal tissues, which are rich in ions, while acidity depended on the length of exposure to leaching due to stem flow.

Studies on changes of element concentration in stem flow while it flows down the trunk are lacking. HANSEN (1995) showed an increase in K content of precipitation with proceeding passage of the tree crown, and in this present study a close correlation between stem flow and bark content occurred for Cu and Mn in *Abies balsamea*, whereas Ca and Zn content of stem flow and bark content were correlated in *Picea rubens* (Tab. 5-4). But data from this study do not allow any conclusion as to whether the correlations of Mn and Zn are due to leaching from the bark or due to the adsorption of both elements by the bark that was previously leached from the needles. Ca and Cu, probably derived from atmospheric deposition (NIHLGÅRD 1970, GODT 1986, SCHMIDT 1987), were either deposited in the canopy and afterwards transported via stem flow along the bark or they were deposited directly on the bark due to mist events.

Tab. 5-4. Spearman correlation coefficient between element content in stem flow and bark of *Abies balsamea* and *Picea rubens*.

	r_s *A. balsamea*	r_s *P. rubens*
K	0.46 *	0.41
Ca	-0.21	0.48 *
Mg	0.01	0.42
Fe	0.15	0.05
Mn	0.69 ***	0.32
Zn	0.06	0.51 *
Cu	0.72 ***	0.15

Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Adsorption on the bark is particularly relevant for heavy metals because of their high tendency to bind to organic surfaces (MAYER 1981, GODT 1986). LÖVESTAM et al. (1990), carrying out X-ray microprobe analysis of transverse sections of *Picea abies*-trunks from Sweden, reported a high concentration of Cu at the surface of the bark, whereas Ca showed a pronounced bark-wood discontinuity as well as a clear ring structure in the wood. While Cu was assumed to be absorbed at the surface of the bark due to pollution, the authors explained Ca in contrast to NIHLGÅRD (1970) and GODT (1986) as an element taking part in the metabolism of the tree. LIN et al. (1995) were able to demonstrate with Zn and Mn-isotopes that were applied on the stem of *Abies balsamea*-seedlings that 63 % of the former and 58 % of the latter was absorbed from the bark. However, 99 % of the elements remained at or near the application sites, with the remainder translocated to roots, other parts of the stem, twigs and needles. On the other hand, when Mn and Zn were applied to shoots, a significant translocation, mainly to the needles, followed. Thus, it can be concluded that once Mn and Zn are deposited on the bark by mist events or by stem flow enriched with leachates from the canopy, more than half can be absorbed, but will not be translocated.

Not only bark, but also soils are progressively leached by acid precipitation (FARMER et al. 1991). Subsequent decreases in soil pH as well as in exchangeable pools of Ca^{2+} and Mg^{2+}, and increases in exchangeable Al^{3+} in the soil are well known consequences (SCHLEGEL et al. 1992, JOHNSON et al. 1994, EDWARDS et al. 1995). This change in soil acidity and the connected shift in ion availability in the soil solution can have an influence on foliar leaching in the canopy (EDWARDS et al. 1995) and thus, a change in element concentration of the stem flow and bark buffer capacity can take place. Studies that quantify the significance of root uptake to element content in the bark are lacking. A study on the sources of 20 trace-elements in the bark of *Populus*, *Quercus*, *Salix*, and *Ulmus* from the Netherlands established that the contents of As, Ce, Cr, Cs, Fe, La, Rb, Sc, Sm, and Th were decisively influenced by the soil (KUIK & WOLTERBEEK 1994). However, the study left open to what extent the elements reached the bark through root uptake or through the deposition of aerosols on the surface. GAUSLAA & HOLIEN (1998) observed a response of the pH of lichens and bark of *Picea abies* twigs to a forest vegetation gradient reflecting the soil nutrient condition at the forest floor.

Epiphytic lichens influence the flux of nutrients in forests not only by altering the element composition of precipitation (Ch. 5.2.5) but also by influencing litter quality and thereby the rate of decomposition of organic matter: While leaves of *Quercus douglasii* contributed 36 - 43 % of N, and 52 - 53 % of P, lichen litter contributed 5 - 14 % of the N but only 2 – 6 % of the P (KNOPS et al. 1996). The rate of decomposition of the oak leaves was significantly affected by the presence of lichens, which caused slower release of N and P from the oak leaves (KNOPS et al. 1996). The authors concluded that this slower decomposition was not a direct result of the P immobilization in the lichen thallus, but due to an attraction of specific decomposers by lichen litter. However, the release of N and P from the litter, with or without lichens, was small compared to the soil pool and the flux originating from that pool. Therefore, the decomposition of oak leaves and lichens in the litter layer was not likely to be a substantial source of nutrients for the oak trees (KNOPS et al. 1996). Elements, accumulated in canopy lichens through uptake of deposition are returned to the ground, not only by throughfall, but also

by lichen litter fall. Epiphytes strongly enhance the absorption of atmospheric deposition of N, not only through enriching the throughfall but also by incorporating a large proportion of the nutrient input into new lichen growth (KNOPS et al. 1996). This was not as obvious for P, where atmospheric deposition was much less enhanced.

The influence of wet and dry deposition on leakage of the canopy and the role of epiphytic lichens on that system is described in Ch. 5.2.4 and Ch. 5.2.5 and will not be discussed here any further.

5.2.7 Comparison of different extractants for cations from the bark

Lichens take up elements from wet and dry deposition and from the substrate. However, the availability of ions from the substrate is poorly known. Methods used by several authors in order to determine the relevance of elements in the substrate were concentrated either on only total contents (GAUSLAA 1985, CHIARENZIELLI et al. 1997, HAUCK et al. 2001) or on exchangeable cations (GOWARD & ARSENAULT 2000). Comparative measurements between different extractants were never carried out. Thus, in the present study the extractants H_2O, EDTA, and $SrCl_2$ were verified for their efficiency in releasing cations from the substrate.

H_2O extractions showed the lowest concentrations determined for every element, giving the indication for representing the minimum available element content. $SrCl_2$ extracted most efficiently K, Ca, and Mg, whereas EDTA was the strongest extractant for the heavy metals Fe, Mn, Zn, and Cu. When correlation analyses between lichen cover of the ten most frequent lichen species and extract concentrations were carried out, correlations with $SrCl_2$ showed a higher coefficient of correlation than with EDTA or H_2O for the elements K and Mg. Ca on the other hand did not show any decisive difference between the extractants. Fe, Mn, Zn, and Cu showed the highest coefficients of correlation with EDTA as an extraction media.

The results found in the present study parallel with results of VÁZQUEZ et al. (1999), who extracted cations with $NiCl_2$, EDTA, and $Pb(NO)_2$ from the moss *Fontinalis antipyretica*. $NiCl_2$ was shown to be adequate for metals with a low affinity for the binding sites, whereas EDTA and $Pb(NO)_2$ were more efficient for metals with a medium to high affinity for extracellular binding sites such as Co, Cu and Pb (VÁZQUEZ, et al. 1999). Mg did not differ between the extraction media. BRANQUINHO et al. (1997) found Na_2-EDTA to be an efficient agent for extracting extracellular Cu from *Cladonia portentosa*, *Ramalina fastigiata*, and *Usnea* spp. K, Ca, and Mg were more efficiently extracted by using $NiCl_2$.

Water eluates probably do not give realistic concentration ranges of available elements. Lichens containing secondary metabolites are able to solve higher element concentrations out of their substrate. This was shown by ISKANDAR & SYERS (1972) and ASCASO & GALVAN (1976) who determined higher element concentrations in extractions from rocks with fumarprotocetraric acid than with H_2O.

5.2.8 Influence of tree species on element concentration on the trunk surface

ANOVA revealed a significant effect of the tree species on the element deposition of P, S, K, Na, Mn, Al, Cu, H^+, and NO_3^-; except for NO_3^- all elements were higher concentrated in at least one of the measuring periods in the stem flow of living *Abies balsamea* compared to living *Picea rubens*. NO_3^- was more concentrated in stem flow of the latter species. Correlations were found between the K, Mn, and Cu content of the stem flow and of the bark (Tab. 5-4). The balance of the element content of the bark is generally influenced by 1) adsorptions of ions from the soil, by 2) dry deposition of elements on the trunk surface, by 3) leaching, and/or by 4) absorption of ions by the bark from the stem flow. The importance of each single factor on the balance may be different and depends on the element and on the species. Comparative studies on the mechanism of element deposition in the bark between *Abies balsamea* and *Picea rubens* are lacking. But it can be suspected that due to the faster scaling of the bark of red spruce lower concentrations are achieved compared to the long-lasting bark of balsam fir. LÖVESTAM et al. (1990) were able to demonstrate that elements such as S, K, Mn, and Cu are accumulated in the bark, probably due to pollution. However, the data of this study do not allow a conclusion as to whether the elements were taken up from the trunk directly due to wet or dry deposition or whether they were taken up by roots and translocated into the bark. A lower rate of assimilation in living *Picea rubens* as compared to *Abies balsamea* could be responsible for the higher NO_3^- concentration in the stem flow of the former tree species. NO_3^- assimilation in *Picea abies* canopy was confirmed by EILERS et al. (1992), but comparative studies for the tree species are lacking.

Concentrations of NO_3^-, Ca, Mn, Al, and H^+ were higher in stem flow of dead spruce than of dead fir. A mechanism other than leakage from the bark must be responsible for this phenomenon, as contents of Ca and Mn did not differ in the bark between the dead tree species. Additionally, Mn in stem flow did not correlate with Mn in the bark of *Picea rubens* and also Ca correlated only weakly. NO_3^- as well as Al were only measured in the stem flow. An explanation for the differences in element correlations between the dead tree species can be possibly seen in the higher amount of stem flow on spruce than on fir.

N, C, K, Mg, Mn, Zn, and Cu were more concentrated in the bark of living *Abies balsamea* as compared to living *Picea rubens*, whereas content of Fe and H^+ were higher in the bark of the latter. Crystals with high Mn contents were found in spongy cork cells in the bark of *Abies balsamea*, but not in *Picea rubens*. Mn concentrations were significantly higher in the outer than in the inner bark of *Abies balsamea*. Two reasons could be responsible for the Mn accumulation in the bark of *Abies balsamea*: (1) Accumulation in the cells by direct absorption of dry and wet deposition from the bark, or (2) accumulation in the cells after root uptake from the soil and translocation.

(1) Elevated Mn concentrations in the outer compared to the inner part of the bark of *Fagus sylvatica* were found in northern Germany by SCHMIDT (1987). The author hypothesized an adsorption of Mn from atmospheric deposited particles. Mn is an important air pollutant in North America and is released from car exhaust since it replaced Pb in the 1970s as a gasoline additive in

Canada (NRIAGU 1990, LORANGER & ZAYED 1994, LIN et al. 1995). As Canada is only about 70 km away from Whiteface Mountain, a deposition of Mn from this source is probable. LIN et al. (1995) showed in experiments with balsam fir seedlings that 58 % of Mn applied to the bark was absorbed and remained to 99 % at or near the application site.

(2) Mn is taken up in high rates by roots and has additionally a high mobility within plants (LINDBERG et al. 1979). Mn is taken up selectively and preferentially from roots of *Fagus sylvatica*, whereas *Picea abies* is supposed to have a passive mechanism (MAYER 1981, SCHMIDT 1987). GODT (1986) reported an only moderate discrimination of Mn in root uptake in *Fagus sylvatica*; *Abies* was not investigated. Plant availability of Mn in the soil solution is highly pH dependent (SCHMIDT 1987, KAZDA & ZVACEK 1989). Quantitatively important amounts of Mn are available at pH < 4.5 (MATZNER 1988). The pH of the organic layer and of the mineral horizon at the field site of Whiteface Mountain was about 3.2 and 3.5, respectively. At these pH values soils are supposed to contain only a small reservoir of insoluble Mn-oxides (MATZNER 1988). But pH is not the only factor for determining Mn availability in the soil solution. The origin of the bedrock and thus, the total Mn content in form of Mn oxides in the soil itself is relevant. The dominant bedrock of Whiteface Mountain is metanorthosite (Ch. 2.2), that contains only trace amounts of Mn oxides (LETTENEY 1969). Metanorthosite is a metamorphosed anorthosite, a rock composed of 90 % or more of plagioclase (ISACHSEN et al. 1991), which is poor in Mn. This is reflected by the low Mn contents of the mineral soil at the field site (Tab. 4-19). However, the concentration of Mn in the organic layer is high compared to that of the mineral soil, which may indicate atmospheric Mn deposition or leaching from the canopy. According to LIN et al. (1996) only about 26 % of Mn applied to the soil was translocated from the roots into the stem in balsam fir seedlings, whereas 31 % remained in the roots themselves, 31 % were transported in twigs, as were 12 % in needles. An important factor for element accumulation is the durability of the bark. Scaliness of *Picea rubens* bark is much higher than that of *Abies balsamea* bark. Hence, higher concentrations of elements can be accumulated over time. LÖVESTAM et al. (1990) found in the bark of balsam fir a higher Mn concentration than in the wood of spruce and a minimum-maximum pattern through a bark section. The authors concluded that this pattern might derive from radial channels in the wood.

The translocation of Mn into the bark can not only take place from the soil, but also from the canopy due to Mn uptake from deposition. As LIN et al. (1995) showed in balsam fir seedlings, Mn applied to the shoots was absorbed and translocated, but mainly to the needles (48 %), whereas only 0.2 % was found in the stem. This is in accordance with the results of SCHMIDT (1987) in *Picea abies*. EPSTEIN (1971) and MENGEL (1984) assessed the mobility of absorbed Mn in the phloem only as moderate.

In conclusion, the data do not allow a definite answer whether Mn was accumulated in the bark due to direct absorption or due to uptake from the soil. According to the results of EPSTEIN (1971), MENGEL (1984), and LIN et al. (1995) the possible translocation of Mn from the canopy to the bark can be neglected. However, if Mn was translocated from the soil into the bark, the question why the

Mn content is higher in the outer than in the inner bark remains unanswered, as crystals would have to be formed during the cell development. Thus, the Mn content would have to be even distributed throughout the bark. This, in conjunction with the Mn distribution in the soil, the results of LIN at al. (1995, 1996), and the possible Mn deposition from Canada supports the first hypothesis. However, the low Mn concentration in the incident precipitation of the present work does not support this explanation.

Element concentrations of dead trees between species behaved very similarly. Except for Zn, all other elements were more concentrated in dead fir than in dead spruce. Dead *Picea rubens* contained no elements in higher concentrations in the bark than dead *Abies balsamea*. Although the bark structure plays an important role for element uptake (CHAMBERLAIN 1975, RIEDERER 1991) and the bark of *Picea rubens* seemed more rough than the bark of *Abies balsamea*, the bark of the latter species does not scale as frequently as the bark of *Picea rubens* does. Thus, the bark of the former species stays physiologycally longer active than the one of the latter species. Hence, accumulation can take place over a longer period of time in the bark of *Abies balsamea*. For Zn, no explanation can be provided.

5.2.9 Influence of tree vitality on element concentration on the trunk surface

Tree vitality had a significant influence on element deposition of S, Na, Fe, Al, and conductivity on the trunk surface of the investigated spruce and fir trees as well as of Mn and Cu of fir. NO_3^- had a higher concentration on living spruce in 1999 as compared to dead ones, but this did not apply to fir. All of these elements had a higher concentration on living trees than on dead ones. This might be related to the significantly higher interception of living compared to the dead trees due to the larger canopy surface of the former. This is in accordance with studies carried out in the Harz Mountains by HAUCK (2000) and HESSE (2002).

The more difficult question is why this phenomenon of higher amounts in the stem flow of living trees does not apply to all elements.

If the higher amount of needles is the responsible factor for the higher concentrations of one group of elements, the same mechanism should also affect the other elements in the same way. Thus, a process other than interception is likely to have an antagonizing effect.

NH_4^+, NO_3^-, and P were probably assimilated in significant amounts in the canopy. The assimilation of NH_4^+ in needles of *Picea abies*, *Abies balsamea*, and other trees was demonstrated in several studies (LANG et al. 1976, MATZNER 1988, IBROM 1993, VEITHEN 1996, YAMADA 2001) and has also been shown for NO_3^- (EILERS et al. 1992). In contrast to the uptake of NH_4^+, NO_3^- was assimilated much more slowly (SMITH 1960). The content of NH_4^+ and NO_3^- in the throughfall is regularly reduced in stands of spruce during the time of needle production (MATZNER et al. 1982, VEITHEN, 1996).

The assimilation of P in the canopy of trees is not yet proven but due to microorganisms inhabiting the phyllosphere it is conceivable (ELLENBERG et al. 1986).

In the case of Mg, either uptake from the living trees (SCHLEGEL 1989) or an increased leaching (SLOVIK et al. 1996) of the dead trees could cause the insignificant difference in Mg content in the stem flow of dead vs. living trees.

For K, Ca, and Zn, above-ground uptake has not been reported. A possible explanation why the concentration of these elements in the stem flow of dead and living trees does not differ is more difficult. SLOVIK et al. (1996) found an increasing effect of SO_2 on the throughfall to be true for K and Ca. Furthermore, Mn and Zn concentrations in the throughfall were positively correlated with the NO_x concentration. BALESTRINI et al. (1998) reported a relation between throughfall of K, Ca, and NO_3^- and greater forest damage. Thus, a greater leaching rate of the dead trees due to pollution could explain the similarities in stem flow concentration between the different tree vitalities. But if this is true, a correlation between stem flow and bark would also be expected. This is true only for *Abies balsamea* and K and for *Picea rubens* and Ca and Zn. Hence, no general explanation can be expressed and further investigations would have to be carried out.

Most elements (except for N, Fe, Pb in *Picea rubens* and for Mg, Fe, Zn, Pb, Cu, and H^+ in *Abies balsamea*) differed in their concentration in the bark between dead and living trees. Except for K, Ca, Mg, Mn, and Zn in *Picea rubens* and N and Ca in *Abies balsamea*, all elements were more concentrated in the bark of living trees. The distribution of the elements can be due to either the effect of the stem flow or to the tree metabolism (LÖVESTAM et al. 1990). On balance, no definite explanation can be provided.

ANOVA revealed that bark chemistry was considerably less influenced by tree vitality than the chemical composition of the stem flow (Tab. 4-A38, Tab. 4-A19). This is plausible, as stem flow is directly influenced by changes in interception, whereas bark chemistry is secondarily affected when substances dissolved in the stem flow are deposited on the bark surface.

In conclusion, differences in stem flow chemistry can be explained by the differences in living vs. dead *Abies balsamea* and living vs. dead *Picea rubens* with the hypothesis that due to changed interception a change in stem flow chemistry occurs.

5.3 Possible effects of chemical site factors on lichen vegetation

5.3.1 NO_3^-

Correlation analysis revealed that cover of 12 and 14 lichen species, respectively, decreased in 1999 and/or 2000 with increasing NO_3^- concentration in the stem flow (Tab. 4-20).

An experiment concerning the effect of NO_3^- solutions of different concentrations on the chlorophyll content and on the ergosterol content in *Hypogymnia physodes* (Ch. 4.5) revealed that NO_3^- concentrations between 100 µmol l^{-1} and 10 mmol l^{-1} reduced the contents of chlorophylls a and b, while the ergosterol content remained unaffected compared to the controls. Further, the chlorophyll a : ergosterol ratio decreased with increasing NO_3^- concentration. However, algal cells did not differ in size and number between the various NO_3^-

treatments and controls in the present study (Fig. 4-18). A negative correlation between NO_3^- and chlorophyll content as well as net photosynthesis was reported from studies with transplanted *Ramalina menziesii* from a control site to a polluted one in California by BOONPRAGOB & NASH (1991). The authors concluded that NO_3^- was present in toxic concentrations, as the upper limit of NO_3^- concentration within plant cells is between 3 and 7 µmol g^{-1} (BOONPRAGOB & NASH 1991). Statements about possible concentrations in lichens of the field site on Whiteface Mountain can not be made and further investigations would need to be carried out.

As multiple regression analysis revealed, a relationship between NO_3^- and lichen cover could be established: negative correlations were found for NO_3^- in the stem flow and mean lichen cover on the sample trees.

Assimilation is the responsible mechanism for differences in NO_3^- concentration of the stem flow, whereby (1) assimilation from the needles, or (2) assimilation from the lichen vegetation can be possible reasons. In the first case lichen cover depends on the NO_3^- concentration in the stem flow what means that the higher the NO_3^- concentration is, the lower is the lichen cover. In the second case, NO_3^- concentration decreases with increasing lichen abundance. Both possibilities will be discussed in the following:

(1) Assimilation of NO_3^- by needles of balsam fir was established experimentally by LANG et al. (1976); this finding was confirmed by EILERS et al. (1992) and VEITHEN (1996) in Norway spruce in Germany. LANG et al. (1976) observed a reduced NO_3^- uptake of 50 % compared to NH_4^+ in an experiment with *Platismatia glauca*; SMITH (1960) found a much slower absorption of NO_3^- as compared to NH_4^+ in a study with *Peltigera polydactyla*. Furthermore, a negative influence of NO_3^- on the photobiont in *Hypogymnia physodes* was shown experimentally in the present work.

(2) With increasing height of *Abies balsamea* N content in the thalli of composite epiphytic lichen samples increased (LANG et al. 1980). This could be due to a gradient of N availability, if N is constantly taken up from epiphytes while the rain passes the canopy. Additionally, previous reports indicated a fertilizer effect of NO_3^- solutions when supplied to lichens. KAUPPI (1980) reported an increase in chlorophyll content in *Cladonia stellaris*, a terricolous species of the tundra, when treated with 2.3 mmol l^{-1} NO_3^- in $NaNO_3$ fertilizer. Algal cells increased in number and grew in size. The amounts of NO_3^- measured in the stem flow of the field site on Whiteface Mountain were much lower (Tab. 4-4). Compared to the concentrations mentioned in the work of KAUPPI (1980), a damaging effect would thus, be unlikely.

Epiphytes affect the interception of rain by the forest canopy and the deposition of water and nutrients in throughfall collected beneath the canopy (KNOPS et al. 1996). The authors showed a higher deposition of organic N in the throughfall of *Quercus douglasii* covered with lichens (dominant lichen: *Ramalina menziesii*, with an estimated biomass of 590 kg ha^{-1}) in California compared to uncovered trees, but the deposition of NO_3^- and NH_4^+ was not affected. The estimated biomass of the dominant foliose lichen *Hypogymnia physodes* in the present study (about 50 % of the total biomass of epiphytic lichens belonged to this species) was 180 kg ha^{-1} (for estimates used in the calculations see Tab. 5-5). This amount is much lower compared to the

amount determined by KNOPS et al. (1996) and is also lower compared to the 630 kg ha^{-1} of total lichen biomass with the dominant *Hypogymnia physodes* estimated in a balsam fir forest in New Hampshire by LANG et al. (1980). As KNOPS et al. (1996) did not find a difference of NO_3^- deposition in throughfall between trees with and trees without lichen cover, it may also mean that in the present study lichens do not have an effect on the NO_3^- cycling in the forest system and thus NO_3^- assimilation might depend mostly on trees. Regarding the estimated lichen biomass per tree in the study of LANG et al. (1980), only minor differences occur compared to the amounts estimated in the present work: While in the latter study approximately 1 kg dry weight *Hypogymnia physodes* per tree (160 kg ha^{-1}) was calculated for *Abies balsamea* and approximately 0.25 kg per tree for *Picea rubens* (20 kg ha^{-1}), LANG et al. (1980) determined 0.15 – 0.65 kg total biomass for epiphytic lichens per tree in four 60 – 70-year-old *Abies balsamea* stands, with *Hypogymnia physodes* as the dominant lichen species. Aside from different site conditions, the higher lichen biomass may be due to differences in age. In 20 - 30-year-old stands of *Abies balsamea* LANG et al. (1980) found 5 - 20 g biomass per tree, whereas in a 50-year-old stand were 90 g lichen per tree. The age of the trees on Whiteface Mountain are estimated to be 100 years in the case of fir and 200 years in the case of spruce. Differences in lichen biomass between tree species, as found on Whiteface Mountain in the present study, were confirmed by LIU et al. (2000). The authors found an uneven distribution in lichen biomass on *Picea abies* and *Pinus sylvestris* and trees classified into groups of varying dbh in a boreal coniferous forest in Central Finland. While spruce with a dbh of 15 – 21 cm was inhabited by approximately 1 kg of *Hypogymnia physodes*, pine in the same dbh range carried about 0.5 kg *H. physodes*. Biomass of that species was lower on medium spruce (15 – 21 cm dbh) than biomass on dominant spruce (> 21 cm dbh; 1 kg vs. 3 kg).

Arthonia caesia was one of the two species which did not correlate with the NO_3^- concentration in the stem flow. *Arthonia* spec. is known to be nutrient-sensitive and avoids sites with high N supply (WIRTH 1995). In Germany, an increase of eutrophication led to a distinctive decrease of the genus (WIRTH 1995).

On balance, the question to what extent NO_3^- is the responsible factor for the differences in lichen cover between living fir and living spruce as well as between dead and living spruce on Whiteface Mountain can not be answered clearly.

Tab. 5-5. Estimates used in the calculation of biomass of *Hypogymnia physodes* on *Abies balsamea* and *Picea rubens* on Whiteface Mountain.

	Abies balsamea	*Picea rubens*
Lichen cover [%][a]	11.9 ± 0.49	2.43 ± 0.34
Weight of *H. physodes* [mg cm^{-2} DW][b]	21.8 ± 8.17	21.8 ± 8.17
dbh [cm][c]	22.7 ± 5.21	35.2 ± 12.4
Tree height [cm][d]	1700	2300
Number of trees per ha	161	79

[a], [b], [d]: Arithmetic mean ± standard deviation. [c]: After a height of 700 cm for fir and 1700 cm for spruce a three fold amount of lichen cover was assumed after LANG et al. (1980) and LIU et al. (2000). n: [a] = 74, [b] = 90, [d] = 74.

5.3.2 S

Correlation analysis revealed that cover of *Cladonia coniocraea*, *Micarea prasina*, and *Parmelia saxatilis* decreased with increasing S content in the stem flow. Multiple regression analysis showed that for *Parmelia saxatilis* S did not increase the correlation coefficient when included into the model (Tab. 4-A54). For *Micarea prasina* and *Cladonia coniocraea* S was the most closely correlated element, but with a weak correlation in both cases. *Cladonia* species tolerate higher levels of pollution as compared with other fruticose genera (FOLKESON & ANDERSSON-BRINGMARK 1988, WIRTH 1992, GNÜCHTEL 1997). *Cladonia coniocraea* was found to be the most toxitolerant epiphyte on Long Island, New York (BRODO 1966). *Micarea prasina* was more frequent in a healthy stand with higher amounts of S than in a stand affected by forest dieback with lower S concentration in the Harz Mountains, Germany (HAUCK 2000). *Cladonia coniocraea* as well as *Micarea prasina* do not carry the more pollution-sensitive photobiont *Trebouxia*, but the less pollution-sensitive photobionts *Asterochloris* in the former and micareoid algae in the latter case (COPPINS 1983).

According to HAUCK (2000) there is strong indication that S content in the stem flow affected the epiphytic lichen vegetation in dieback affected *Picea abies* stands in the Harz Mountains, Germany. Acidic S compounds are nowadays a very important site factor for lichens in industrialized countries and its effect on the epiphytes has been shown repeatedly (e.g. NASH 1976, SKYE 1979, LECHOWICZ 1982, SCOTT & HUTCHINSON 1987, HALLINGBÄCK & KELLNER 1992, BALAGUER et al. 1997, PIERVITTORI et al. 1997). SO_2 is the most stable S compound at high temperatures and most S originating from combustion processes is emitted into the atmosphere as SO_2 (SCHMIDT 1972, SAUNDERS & WOOD 1973). About half of the SO_2 is removed from the atmosphere by dry deposition without changing its oxidation state (GARLAND 1978, PLATT 1978). Under dry conditions SO_2 has no effect on lichen thalli (TÜRK et al. 1974). In solution SO_2 undergoes a series of equilibrium reactions depending on temperature and pH (SAUNDERS & WOOD 1973). The SO_2 sensitivity of lichens is strongly influenced by their water content. Experiments were carried out with dissolved SO_2 (PUCKETT et al. 1977, NIEBOER et al. 1984), $H_2SO_3^-$ (HÄLLGREN & HUSS 1975, GARTY et al. 1995), and $S_2O_5^{2-}$ (HILL 1971, TÜRK et al. 1974) and

revealed severe physiological damages and biochemical changes in lichens such as loss of membrane integrity (FIELDS & CLAIR 1984), reduction of photosynthesis with breakdown of chlorophylls (TÜRK et al. 1974) and reduction of N_2 fixation (HALLINGBÄCK & KELLNER 1992). Also decreased ATP concentration in *Ramalina lacera* (SILBERSTEIN et al. 1990, 1996) and enhanced ethylene production (GARTY et al. 1995, KAUPPI et al. 1998) in *Bryoria fuscescens*, *Cladonia stellaris*, *Hypogymnia physodes*, and *Usnea hirta* was found.

As for the present study, it is improbable that the differences in lichen cover between the different tree species and their variants on Whiteface Mountain can be explained by the S concentration in the stem flow, as they were by the data from the Harz Mountains, Germany (HAUCK 2000); element content of S (and NO_3^-) is approximately 10 times lower on Whiteface Mountain (Tab. 5-6); A number of lichen species growing on Whiteface Mountain were also found in the Harz Mountains (e.g. *Bryoria fuscescens*, *Chaenotheca ferruginea*, *Cladonia coniocraea*, *Cladonia digitata*, *Cladonia pyxidata*, *Hypocenomyce scalaris*, *Hypogymnia physodes*, *Hypogymnia tubulosa*, *Lepraria jackii*, *Micarea prasina*, *Mycoblastus fucatus*, *Platismatia glauca*) and thus, are able to withstand high S concentrations.

Tab. 5-6. Comparison of element content of NO_3^- and S and pH concentration in the stem flow of Whiteface Mountain and the Harz Mountains, Germany. Concentration of NO_3^- and S in [µmol l^{-1}].

	Year[a]	Whiteface Mountain				Harz Mountains	
		R[b]	DR[c]	B[d]	DB[e]	R[f]	DR[g]
NO_3^-	1	15.8 ± 13.3	5.40 ± 2.06	2.26 ± 1.29	3.24 ± 1.34	205 ± 86.7	61.1 ± 17.5
	2	0.76 ± 1.15	0.24 ± 0.22	0.15 ± 0.17	0.21 ± 0.16	239 ± 36.8	80.6 ± 8.0
S	1	18.0 ± 6.92	11.6 ± 2.49	28.6 ± 7.58	11.4 ± 2.50	411 ± 94.8	282 ± 81.9
	2	13.3 ± 2.75	7.70 ± 2.57	16.6 ± 4.37	5.93 ± 2.94	153 ± 20.6	91.7 ± 21.7
pH	1	3.74 ± 0.10	4.17 ± 0.11	3.83 ± 0.08	4.35 ± 0.14	4.19 ± 0.20	4.15 ± 0.20
	2	3.83 ± 0.10	4.18 ± 0.13	3.85 ± 0.12	4.24 ± 0.15	3.68 ± 0.41	3.72 ± 0.88

[a]: Year of measurements: Whiteface Mountain: 1 = 1999, 2 = 2000; Harz Mountains: 1 = 1995, 2 = 1997/1998. [b]: living *Picea rubens*, [c]: dead *P. rubens*, [d]: living *Abies balsamea*, [e]: dead *A. balsamea*, [f]: healthy *P. abies*, [g]: dead *P. abies*.

Also other studies revealed that damages that occurred in lichen thalli treated with simulated acid rain, had concentration ranges similar to those measured in the Harz Mountains. A depression in photosynthetic capacity occurred at SO_4^{2-} concentrations of 100 µmol l^{-1} but not at 6 µmol l^{-1} in *Cladonia stellaris* when treated with artificial rain at pH 4.0 (LECHOWICZ 1982). Daily spraying with 10 ml 300 µmol l^{-1} SO_4^{2-} at pH 3.2 for two weeks caused morphological and chemical alterations in the upper cortex of *Pseudevernia furfuracea* (PIERVITTORI et al. 1997). The fixation of N_2 was reduced in *Peltigera aphthosa* (containing pollution-sensitive cyanobacteria as secondary photobionts) under semi-natural conditions with simulated rain containing 150 µmol l^{-1} SO_4^{2-} (HALLINGBÄCK & KELLNER 1992).

5.3.3 Ca, Mg

Ca concentration in stem flow did not differ significantly between *Abies balsamea* and *Picea rubens*. Nevertheless, Ca correlated negatively with lichen cover of seven lichen species. Multiple regression analysis showed that Ca had no significant effect when it was included into the model with NO_3^- (Tab. 4-A54). Negative effects of Ca in concentration ranges similar to those in the present study are not known, and investigations are lacking. The possible uptake of Ca by lichens can be ruled out, as several lichen species that also occurred in the plot on Whiteface Mountain (i. e. *Evernia mesomorpha*, *Hypogymnia* spec., *Platismatia glauca*, *Pseudevernia cladonia*, and *Usnea* spec.) lost Ca when treated with simulated rain under laboratory conditions (LANG et al. 1976). The lichens used in the study of LANG et al. (1976) grew – similar to the present study – on *Abies balsamea*.

The lichen cover of *Parmelia saxatilis* was negatively correlated with the element content of Mg in the stem flow, but Mg did not enhance the correlation coefficient compared to Mn when multiple correlation analysis was carried out (Tab. 4-A54). At least on tree surfaces, Mg is usually associated with Ca and their occurrence is correlated with pH. As experimental studies are rare (as in the case of Ca), direct effects of Mg on the physiology of lichen species can not be discussed.

5.3.4 Mn

Cover of four lichen species decreased with increasing Mn concentration in stem flow when correlation analysis was carried out. In the case of *Mycoblastus sanguinarius* and *Parmelia saxatilis* multiple correlation analysis showed that Mn in the stem flow had the strongest influence on lichen cover (Tab. 4-A54). Weak negative correlations also occurred between nine lichen species and total Mn content in the bark, whereby the coefficient of correlation never exceeded 0.44. Multiple correlation analysis was not carried out, as no satisfying linearization was found. That lichens are able to accumulate metals from their substratum and surrounding environment was confirmed by JAMES (1973), TUOMINEN & JAAKKOLA (1973), SLOOF & WALTERBEEK (1993), and ARMSTRONG (1997).

A negative effect of Mn in the substrate on the germination rate of soredia of *Hypogymnia physodes* was established by HAUCK et al. (2001). Mn in the Bold's basal medium on agar plates of 3 mM reduced the germination rate by 82 % after an 8 day treatment. Further studies revealed that the chlorophyll a and b content was reduced in germinated soredia exposed to Mn on agar plates due to smaller and partly collapsed *Trebouxia* cells with reduced chloroplasts (HAUCK et al. 2002). Fungal hyphae were shortened and swollen with a significant lost of P. Disintegrated cell walls occurred in both algal and fungal cells.

Incubation experiments with 5 mM Mn solutions with thalli of *Alectoria sarmentosa*, *Bryoria fuscescens*, and *Hypogymnia physodes* revealed a Mn uptake into the cortex (Paul unpubl.). Mn concentrations in the former two lichens were lower than in *Hypogymnia physodes*. Explanations were suspected in chemical differences of cell walls as concluded from CHETTRI et al. (1997, 1998)

after experiments with two *Cladonia* species, in differences of matrix material (ANGLESA et al. 1982, GREENHALGH & Whitfield 1987), or in a higher efflux of Ca into the incubation medium from *Alectoria* and *Bryoria*.

When *Lasallia pustulata*, a saxicolous lichen, was exposed ten times during four weeks for a few minutes each to 9 µmol l^{-1} $MnCl_2$, Mn was effectively taken up into the thallus (ASCASO & FORTUN 1981), but the enhanced Mn content in the thallus of the treated samples compared to the control (0.64 vs. 0.36 µmol g^{-1} DW) did not cause any changes in the ultrastructure of the fungal or algal cells. After exposure of *Cladonia rangiferina* to 10 and 100 mM Mn solution for 90 min, BURTON et al. (1981) established slight K^+ losses. Significant K^+ losses only occurred after an exposure to a 1 M solution. 2 – 6 mM of $MnSO_4$ exposed for 2 h exchanged between 50 – 70 % of total thallus K^+ in *Peltigera canina* (GOYAL & SEAWARD 1982). WILSON & JONES (1984) found Mn to be immobilized as Mn oxalate crystals by *Pertusaria corallina* growing on Mn-bearing rocks. As for the results in the present study, Mn in the stem flow never exceeded a concentration of approximately 18 µmol l^{-1} in any of the measuring periods, while total Mn content determined in the bark was highest in *Abies balsamea* of about 30 µmol g^{-1}. In the bark of *Picea rubens* a Mn concentration of only about 8 µmol g^{-1} DW was achieved. Thus, Mn is affecting epiphytes when applied in high concentrations, but to what extent it affects lichens in concentration ranges as determined in the stem flow and bark in the present study is not clear.

The Mn content in crystals measured in the bark *Abies balsamea* in the present study was much higher compared to Mn concentrations used by BURTON et al. (1981), GOYAL & SEAWARD (1982), and HAUCK et al. (2002). However, damaging effects can be ruled out as Mn in the crystals is immobilized.

5.3.5 Fe

Lichen cover of *Cladonia coniocraea* correlated negatively with Fe in the stem flow; Fe did not enhance the correlation coefficient compared to S when multiple correlation analysis was carried out (Tab. 4-A54). Thus, it is unlikely that Fe in stem flow has an effect on lichen cover, especially as Fe content in lichen thalli can be very high (up to 56 µmol g^{-1} DW in *Hypogymnia physodes* growing on *Fraxinus excelsior* under the influence of elutions from barb wires) without causing thallus damage (SEAWARD 1974). Correlation between total Fe content in the bark and lichen cover revealed a decrease of the latter with increasing Fe content for seven species in the present study. In investigations, carried out by HAUCK et al. (2000) in a stand of *Picea abies* in the Harz Mountains, Germany, a similar amount of 2 µmol l^{-1} Fe was measured in the stem flow, whereas a lower content of Fe in the bark was determined in the trees on Whiteface Mountain as compared to those in the Harz Mountains (1 vs. 9 µmol g^{-1}). No significant correlation was found on the study site in Germany between Fe content and lichen cover.

On balance, there is indication that NO_3^- in the stem flow might affect epiphytic lichen vegetation. Whether S, Ca, and Mg in the stem flow and Mn and Fe in stem flow and bark had an additional effect on lichen vegetation is not yet clear.

5.4 Influence of microclimate on lichen vegetation

The significance of climatic conditions, such as light, water relations, and temperature on lichens has been discussed frequently (e.g. CULBERSON 1955, HALE 1955, BRODO 1961, LARSON 1979, SNELGAR et al. 1980, BENEDICT 1990, HALONEN et al. 1991, HYVÄRINEN 1992, LANGE & GREEN 1996, GAUSLAA & SOLHAUG 1998, CAMPBELL & COXSON 2001). It was pointed out repeatedly that microclimate is an important site factor determining the distribution of epiphytic lichens (KERSHAW 1985, SCHÖLLER 1991, RIKKINEN 1995).

None of the microclimatic parameters studied at the field site on Whiteface Mountain differed between the tree species *Abies balsamea* and *Picea rubens* nor between living and dead trees. Differences in water-holding capacity of the bark between tree species as established by KALGUTGAR & BIRD (1969) (with *Pinus albicaulis* and *Larix lyallii*, with a higher capacity on the former) could not be confirmed in the present study. Expected differences in higher light influx, evaporation, temperature and a lower humidity on the dead than on the living trees due to the lower needle mass were not found. This agrees with RENHORN et al. (1997), who transplanted thalli of *Platismatia glauca* and *Lobaria pulmonaria* to the lower canopy of a mature *Picea abies* forest in six different distances from a clearcut. At the forest edge the light intensity was 4.3 times higher than in the stand. As results showed, lichen growth and lichen vitality (measured as fluorescence and chlorophyll content) were unaffected by the distance from the edge, although thallus water content revealed clear differences in both number and length of wetting and drying cycles. The authors attributed the lacking difference of growth and vitality to only minor differences in air temperature and relative humidity between the forest edge and the interior. In the study on Whiteface Mountain dense young growth of balsam fir might explain why the loss of needles and branches of the dead trees did not result in brighter, drier, and warmer microhabitats. Further, the water-holding capacity of the bark showed no significant difference between living and dead trees of both species. A trend towards lower values was determined for the dead trees compared to living ones. This disagrees with HAUCK et al. (2000), who found increasing water-holding capacity with declining tree vitality in the bark of *Picea abies* in the Harz Mountains, Germany. Since none of the microclimatic parameters differed between tree species nor between dead and living trees, they can not be decisive for the lichen distribution between the trees.

Nevertheless, correlations were found between cover values of single lichen species and microclimatic parameters. This might indicate that microclimate may have a small-scale effect on the distribution of individual species. Unlike most cyanobacterial forest lichens, which are indicators of long ecological continuity (ROSE 1976, 1988, 1992), green-algal lichens have distinct and different niches of varying width along a gradient of ecological continuity (GAUSLAA & SOLHAUG 1996). In the present study, cover of *Loxospora ochrophaea* correlated strongly negatively with evaporation, while cover of *Bryoria nadvornikiana* correlated weakly in the same way with evaporation and light influx. As both species are known to prefer humid and shady habitats (BRODO & HAWSKWORTH 1977, WIRTH 1995, BRODO et al. 2001), these correlations might be causal. Furthermore, *Arthonia caesia*, a species preferring very humid and

shady habitats, occured more frequently on the darkest trees compared to the trees with the highest light influx. Short exposures to high light causes a reversible photoinhibition of photosynthesis of different patterns amongst several lichen species, such as *Evernia prunastri*, *Hypogymnia physodes*, *Parmelia saxatilis*, *Platismatia glauca*, *Pseudevernia furfuracea*, and *Ramalina farinacea* (MANRIQUE et al. 1993) as well as *Stereocaulon* spec. (COXSON 1987) and chlorophyll degradation (GAUSLAA & SOLHAUG 1996). The negative correlation between lichen cover of *Bryoria nadvornikiana* and relative humidity, however, is probably not causal, as it contradicts the known ecological preferences of this lichen species and the negative correlations found with evaporation and light.

In contrast to *Bryoria nadvornikiana*, *B. capillaris* and *B. furcellata* as well as the *Usnea* species are more light-demanding and less humidity-dependent, although they avoid dry habitats (BRODO & HAWKSWORTH 1977, WIRTH 1995, CAMPBELL & COXSON 2001). This is in accordance, firstly, with the weak positive correlation found between lichen cover and light influx and, secondly, with the higher occurrence of *Usnea* spec. on the trees with the lowest evaporation compared to those with the highest evaporation. This is also true for the cover of *Evernia mesomorpha* and *Pseudevernia consocians* and the light influx. All these lichens contain secondary metabolites, such as atranorin, usnic acid or melanins which are effective in absorbing UV-B radiation and thus, enable the lichens to grow in places with high irradiance (RIKKINEN 1995). *Lecidea nylanderi* occurred more frequently on trees with the highest light influx compared to the darkest trees. This agrees with its ecology described in the literature: The species grows in light-flooded forests (WIRTH 1995).

Cover of *Evernia mesomorpha* and *Pseudevernia consocians*, growing preferentially on light-flooded sites, was negatively correlated with the water-holding capacity of the bark, indicating a preference for dryer habitats. In general, a higher water-holding capacity of the bark is supposed to enable the lichens to prolong the time of physiological activity after wet deposition due to a delay of desiccation (BUTIN 1954, MÜLLER 1981).

In conclusion, microclimatic conditions showed a weak influence on lichen cover of single epiphytes on Whiteface Mountain, whereby the coefficient of correlation never exceeded 0.4 (except for *Loxospora ochrophaea* with $r = -0.47$). Thus, it can be concluded that, although the microclimate may affect individual species, it is unlikely that the microclimate alone causes the differences in lichen cover between *Abies balsamea* and *Picea rubens* and between living and dead trees.

6 Conclusion

Lichens were considerably more frequent on living *Abies balsamea* compared to living *Picea rubens* and on dead *P. rubens* more frequent than on living *P. rubens*. However, microclimatic parameters did not differ between the living tree species nor between dead and living trees. As differences in epiphytic lichen diversity between dead and living fir as well as dead spruce and dead fir were considerably smaller, it infers that one or more site factors limiting lichen diversity on living spruce were apparently not operative on living fir. The much smaller difference in epiphytic lichen diversity between dead and living fir than between dead and living spruce suggests that microclimatic site conditions, such as photon flux density, evaporation, or relative humidity, were not the decisive site factors. Lichen diversity should increase equally on spruce and on fir with declining tree vitality if changes in microclimate due to needle loss were decisive.

Thus, physico-chemical factors of the substrate are more likely to be decisive for the small-scale distribution of epiphytic lichens within the sample plot. These factors could be the element content or water-holding capacity of the bark (GAUSLAA 1995, HAUCK et al. 2000, 2001) or the element content of stem flow (FARMER et al. 1991, HAUCK & RUNGE 1999). Results may indicate an influence of NO_3^- in the stem flow on lichen cover. Living spruce with a lower lichen frequency than dead spruce or living fir had a higher NO_3^- concentration in the stem flow than the two latter variants, whereas the NO_3^- concentration in the stem flow of dead spruce and living fir with the higher lichen frequency was lower compared to concentrations in stem flow of living spruce. As correlation analysis revealed, lichen cover of a number of species decreased with increasing NO_3^- concentration, and a damaging effect was confirmed experimentally with thalli of *Hypogymnia physodes*. However, since results of e.g. LANG et al. (1976) indicated an effect of NO_3^- assimilation by lichens, the epiphytes could also be decisive for concentrations in stem flow. Concentration of S in the stem flow was, in contrast to studies carried out in the Harz Mountains, of small importance on Whiteface Mountain. Only few correlations with low coefficients of correlation between element content of the bark as well as water-holding capacity and lichen cover occurred and thus, are probably of minor importance for lichen distribution.

However, scaling frequency of the bark between the two tree species might have to be taken into account. *Picea rubens*, possessing a more scaly bark than *Abies balsamea* might loose the bark more frequent than the latter. According to GOUGH (1975), the rate of bark scaling appeared to be the most important substrate feature determining the abundance of epiphytic growth on *Pseudotsuga menziesii* and *Abies lasiocarpa* in Colorado.

7 Abstract

Epiphytic lichen distribution on the trunks of living and dead *Picea rubens* as well as on the trunks of living and dead *Abies balsamea* and its dependency on chemical and microclimatic site factors was studied in a spruce-fir forest on Whiteface Mountain, New York, U.S.A.

Epiphytic lichen diversity was considerably higher on living fir compared to living spruce. Dead spruce had a more diverse epiphytic lichen vegetation than living spruce. *Arthonia caesia* was the dominant lichen species, except for dead fir, where *Hypogymnia physodes* was most common.

Stem flow contained more P, S, K, Na, Mn, Al, and Cu in living fir than in living spruce; The latter species had higher NO_3^- and H^+ concentrations in the stem flow. A lower rate of assimilation in living spruce than in fir could be responsible for the higher NO_3^- concentrations in the stem flow of the former species. Concentrations of NO_3^-, Ca, Mn, Al, and H^+ were higher in the stem flow of dead spruce than of dead fir.

Concentrations of S, Na, Fe, and Al as well as conductivity were higher in the stem flow of living spruce compared to dead spruce. Mn and Cu concentrations in stem flow of living fir were higher compared to dead fir. A reduced interception from the atmosphere as a consequence of needle loss is seen as the main cause for the element distribution. NO_3^- had a higher concentration on living spruce in 1999 compared to dead ones, but this did not apply to fir.

Higher element concentrations in the bark of living fir were found for N, K, Mg, Mn, Zn, Cu, and H^+ compared to living spruce, whereas Fe was more highly concentrated in the bark of the latter. Element concentrations were similar on dead trees of both species, with all elements being slightly higher concentrated in dead fir than in dead spruce (except for Zn). The balance of the element content of the bark is generally influenced by 1) adsorption of ions from the soil, by 2) dry deposition of elements on the trunk surface, by 3) leaching and/or by 4) absorption of ions by the bark from the stem flow. The importance of each single factor on the balance may be different and depends on the element and on the species. It can be suspected that due to the lower scaling frequency of fir bark higher concentrations are achieved compared to the concentrations in the short-lasting spruce bark. For Zn, no explanation can be provided.

Most elements differed in their concentration in the bark between dead and living trees. K, Ca, Mg, Mn, Zn, and H^+ were more highly concentrated in the bark of dead spruce, whereas only N and Ca were more concentrated in the bark of dead fir, each related to the living counterpart. The distribution of the elements can be either due to affections of the stem flow or due to the tree metabolism.

A number of correlations were found between NO_3^- concentration of the stem flow and cover of lichen species. ANOVA revealed the strongest impact of NO_3^- on cover of *Flavopunctelia soredica*, *Hypogymnia physodes*, *Usnea* spec., and *Platismatia glauca*. Additionally, NO_3^- was found experimentally to decrease the chlorophyll a and b contents of *Hypogymnia physodes* compared to the controls at concentrations between 100 µmol l^{-1} and 10 mmol l^{-1}, whereas ergosterol concentrations remained unaffected. The chlorophyll a : ergosterol ratio was lower under the influence of NO_3^- compared to the controls.

Correlations of S, Ca, Mg, Mn, and Fe content of stem flow with lichen cover were possibly coincidental. For Ca, Mg, and Fe, ANOVA revealed no influence of the element on lichen cover. However, S and Mn correlated most closely but with weak correlation coefficients with *Micarea prasina* and *Cladonia coniocraea* in the case of S as well as with *Mycoblastus sanguinarius* and *Parmelia saxatilis* in the case of Mn. Causal relationships can be ruled out in these cases, as some of the same lichen species, found on Whiteface Mountain, grow also in the Harz Mountains where the S-deposition is higher. For Mn, the damaging influence on soredia of *Hypogymnia physodes* was demonstrated in incubation and culture experiments in previous studies of our working group. However, concentrations measured in the stem flow of the present work were considerably lower than in the stem flow of the Harz Mountains and than in the experimental studies, respectively.

Element concentrations of Mn and Fe in the bark were of minor importance when correlated with lichen cover. High amounts of Mn measured in the bark of fir do not affect lichen growth, as the element was found immobilized in crystals.

None of the microclimatic parameters differed between fir and spruce, nor between living and dead trees, because of dense young growth. Microclimatic site factors showed a weak influence on lichen cover of single epiphytes. *Loxospora ochrophaea* correlated negatively with evaporation, whereas cover of *Bryoria nadvornikiana* correlated weak in the same way with evaporation and light. *Arthonia caesia* occurred more frequent on the darkest trees compared to the trees with the highest light influx. Cover of *Bryoria capillaris* and *B. furcellata*, *Evernia mesomorpha*, *Lecidea nylanderi*, *Pseudevernia consocians* as well as *Usnea* spec. and light were positively correlated. Thus, it can be concluded that, although microclimate affects individual species, it is improbable that the site factor alone causes the differences in lichen cover between fir and spruce and living and dead trees.

Overall, the results support the hypothesis that a the lack of needles on dead trees leads to a reduced pollutant load on the trunk surface and enables a more diverse epiphytic lichen vegetation compared to living trees. Furthermore, NO_3^- in the stem flow seems to influence the lichen cover and might provide an explanation why lichens grow more frequent on fir than on spruce and on dead spruce more frequent than on the living counterpart. However, since an assimilation by lichens could be confirmed by other working groups, epiphytes could also be decisive for concentrations in stem flow. Influences of the microclimate can not be ruled out for individual lichen species, whereas the bark content seems to be of minor importance.

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10 Appendix

Tab. 4-A1. Mean cover of lichen vegetation on living *Abies balsamea* (B) compared to living *Picea rubens* (R).

	R	B	
Species more frequent on B:			
Bryoria capillaris	0.01 ± 0.06	0.20 ± 0.35	**
Evernia mesomorpha	0.00 ± 0.00	0.09 ± 0.18	**
Flavopunctelia soredica	0.22 ± 0.20	0.55 ± 0.45	***
Haematomma ochroleucum	0.18 ± 0.82	2.25 ± 4.35	***
Hypogymnia physodes	2.19 ± 4.05	12.2 ± 10.1	***
Japewia subaurifera	0.11 ± 0.43	0.43 ± 0.74	**
Loxospora cismonica	0.00 ± 0.00	0.26 ± 1.06	*
Mycoblastus sanguinarius	0.74 ± 1.81	5.66 ± 7.61	***
Parmelia saxatilis	0.02 ± 0.07	1.32 ± 3.22	***
Platismatia glauca	0.11 ± 0.19	4.13 ± 5.82	***
Pseudevernia cladonia	0.07 ± 0.14	0.26 ± 0.27	***
Pseudevernia consocians	0.16 ± 0.82	0.27 ± 0.33	***
Ropalospora chlorantha	0.00 ± 0.00	0.34 ± 1.16	*
Usnea spec.	0.04 ± 0.09	0.47 ± 0.54	***
Species more frequent on R:			
Hypocenomyce friesii	2.76 ± 5.51	0.08 ± 0.42	***
Hypocenomyce scalaris	0.48 ± 1.78	0.00 ± 0.00	***
Mycoblastus fucatus	0.75 ± 4.52	0.27 ± 0.58	**

(Cont.)

(Cont. Tab. 4-A1)

	R	B
Indifferent species:		
Alectoria sarmentosa	0.11 ± 0.19	0.09 ± 0.16
Arthonia caesia	18.1 ± 18.8	18.2 ± 22.6
Bryoria furcellata	0.03 ± 0.12	0.71 ± 3.77
Bryoria fuscescens	0.11 ± 0.20	0.40 ± 0.81
Bryoria nadvornikiana	0.07 ± 0.16	0.03 ± 0.10
Bryoria subcana	0.02 ± 0.07	0.13 ± 0.33
Bryoria trichodes	0.01 ± 0.04	0.01 ± 0.04
Chaenotheca ferruginea	0.34 ± 1.68	0.00 ± 0.00
Cladonia coniocraea	1.18 ± 3.66	0.61 ± 1.97
Cladonia digitata	0.01 ± 0.06	0.01 ± 0.04
Cladonia fimbriata	0.00 ± 0.00	0.01 ± 0.04
Cladonia macilenta s.l.	0.01 ± 0.06	0.02 ± 0.07
Cladonia pyxidata s.l.	0.01 ± 0.04	0.00 ± 0.00
Cladonia squamosa	0.85 ± 2.41	0.41 ± 1.73
Hypogymnia krogiae	0.00 ± 0.00	0.14 ± 0.82
Hypogymnia tubulosa	0.00 ± 0.00	0.01 ± 0.04
Imshaugia aleurites	5.36 ± 8.83	4.58 ± 5.31
Lecanora impudens	0.01 ± 0.04	0.15 ± 0.82
Lecanora pulicaris	0.00 ± 0.00	0.03 ± 0.16
Lepraria jackii	5.27 ± 8.26	4.93 ± 6.63
Lecidea nylanderi	6.86 ± 8.02	9.5 ± 10.51
Loxospora ochrophaea	0.00 ± 0.00	2.12 ± 7.53
Micarea melaena	0.19 ± 0.77	0.63 ± 3.70
Micarea prasina	0.88 ± 4.26	0.02 ± 0.09
Mycoblastus alpinus	0.05 ± 0.20	0.06 ± 0.21
Parmeliopsis capitata	0.02 ± 0.07	0.00 ± 0.00

Arithmetic mean ± standard deviation; calculated from mean values of 2 relevés per tree. n = 37. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A2. Mean cover of lichen vegetation on dead *Abies balsamea* (DB) compared to dead *Picea rubens* (DR).

	DR	DB	
Species more frequent on DB:			
Haematomma ochroleucum	0.81 ± 4.12	4.14 ± 7.96	**
Hypogymnia physodes	2.67 ± 4.78	11.5 ± 9.89	***
Japewia subaurifera	0.02 ± 0.07	0.59 ± 2.52	*
Lepraria jackii	3.55 ± 3.91	6.69 ± 7.61	*
Lecidea nylanderi	2.44 ± 5.11	4.75 ± 5.99	**
Loxospora ochrophaea	1.39 ± 5.76	5.66 ± 11.0	***
Mycoblastus sanguinarius	0.51 ± 1.50	4.30 ± 6.07	***
Parmelia saxatilis	0.95 ± 2.97	1.77 ± 2.62	**
Platismatia glauca	0.28 ± 0.30	3.70 ± 6.22	***
Ropalospora chlorantha	0.04 ± 0.25	1.99 ± 5.48	***
Usnea spec.	0.20 ± 0.20	1.26 ± 2.99	**
Species more frequent on DR:			
Alectoria sarmentosa	0.14 ± 0.16	0.06 ± 0.14	*
Arthonia caesia	18.4 ± 15.3	9.46 ± 17.2	**
Cladonia digitata	0.17 ± 0.47	0.05 ± 0.25	*
Cladonia squamosa	3.31 ± 6.40	1.34 ± 5.84	*
Hypocenomyce friesii	5.70 ± 9.98	0.00 ± 0.00	***
Hypocenomyce scalaris	1.11 ± 4.45	0.00 ± 0.00	*
Imshaugia aleurites	5.30 ± 8.72	0.43 ± 1.08	***
Micarea melaena	1.78 ± 4.39	0.12 ± 0.45	**

(Cont.)

(Cont. Tab. 4-A2)

	DR	DB
Indifferent species:		
Bryoria capillaris	0.07 ± 0.14	0.19 ± 0.31
Bryoria furcellata	0.05 ± 0.12	0.13 ± 0.23
Bryoria fuscescens	0.18 ± 0.23	0.31 ± 0.51
Bryoria nadvornikiana	0.05 ± 0.10	0.10 ± 0.25
Bryoria subcana	0.03 ± 0.10	0.03 ± 0.08
Bryoria trichodes	0.01 ± 0.04	0.00 ± 0.00
Calicium glaucellum	0.55 ± 3.29	0.00 ± 0.00
Chaenotheca chrysocephala	0.38 ± 1.49	0.47 ± 2.88
Chaenotheca ferruginea	0.28 ± 1.64	0.00 ± 0.00
Cladonia coniocraea	3.18 ± 5.43	1.05 ± 1.33
Cladonia fimbriata	0.24 ± 0.91	0.07 ± 0.19
Cladonia macilenta s.l.	0.11 ± 0.50	0.03 ± 0.11
Cladonia pyxidata s.l.	0.09 ± 0.41	0.07 ± 0.29
Evernia mesomorpha	0.06 ± 0.11	0.12 ± 0.17
Flavopunctelia soredica	0.35 ± 0.25	0.65 ± 1.22
Hypogymnia krogiae	0.02 ± 0.09	0.89 ± 3.13
Lecanora pulicaris	0.00 ± 0.00	0.01 ± 0.04
Lecidea leprarioides	0.00 ± 0.00	1.05 ± 6.33
Micarea botryoides	0.07 ± 0.41	0.00 ± 0.00
Micarea prasina	1.89 ± 5.16	0.11 ± 0.43
Mycoblastus alpinus	0.00 ± 0.00	0.01 ± 0.04
Mycoblastus fucatus	0.05 ± 0.18	0.17 ± 0.44
Parmeliopsis capitata	0.00 ± 0.00	0.01 ± 0.04
Pseudevernia cladonia	0.28 ± 0.26	0.22 ± 0.25
Pseudevernia consocians	0.21 ± 0.38	0.39 ± 0.90

Arithmetic mean ± standard deviation; calculated from mean values of 2 relevés per tree. n = 37. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A3. Maxima of cover values (in %) of epiphytic lichen species on living (B) and dead (DB) *Abies balsamea* as well as living (R) and dead (DR) *Picea rubens*.

	B	R	DB	DR
Alectoria sarmentosa	0.50	0.75	0.50	0.50
Arthonia caesia	81.5	77.5	64.0	42.5
Bryoria capillaris	1.50	0.25	1.25	0.50
Bryoria furcellata	23.0	0.50	1.00	0.50
Bryoria fuscescens	3.50	0.75	2.25	1.00
Bryoria nadvornikiana	0.50	0.75	1.25	0.25
Bryoria subcana	1.50	0.25	0.25	0.50
Bryoria trichodes	0.25	0.25	0.00	0.25
Calicium glaucellum	0.00	0.00	0.00	20.0
Chaenotheca chrysocephala	0.00	0.00	17.5	7.75
Chaenotheca ferruginea	0.00	10.00	0.00	10.0
Cladonia coniocraea	9.00	19.00	5.00	20.0
Cladonia digitata	0.25	0.25	1.50	2.50
Cladonia fimbriata	0.25	0.00	1.00	5.50
Cladonia macilenta s.l.	0.25	0.25	0.50	3.00
Cladonia pyxidata s.l.	0.00	0.25	1.50	2.50
Cladonia squamosa	10.5	10.0	35.5	30.3
Evernia mesomorpha	0.50	0.00	0.50	0.25
Everniastrum catawbiense	0.00	0.00	0.00	0.00
Flavopunctelia soredica	2.00	0.75	7.50	1.25
Graphis scripta	0.00	0.00	0.00	0.00
Haematomma ochroleucum	16.0	5.00	30.0	25.0
Hypocenomyce friesii	2.50	22.0	0.00	40.0
Hypocenomyce scalaris	0.00	10.3	0.00	25.0
Hypogymnia krogiae	5.00	0.00	15.0	0.50
Hypogymnia tubulosa	0.25	0.00	0.00	0.00
Hypogymnia physodes	40.0	20.0	40.0	25.0
Imshaugia aleurites	18.5	42.5	5.50	37.5
Japewia subaurifera	3.25	2.50	15.0	0.25

(Cont.)

(Cont. Tab. 4-A3)

	B	R	DB	DR
Lecanora impudens	5.00	0.25	0.00	0.00
Lecanora pulicaris	1.00	0.00	0.25	0.00
Lepraria jackii	27.5	30.0	35.0	12.5
Lecidea leprarioides	0.00	0.00	38.5	0.00
Lecidea nylanderi	31.5	27.5	19.5	25.0
Loxospora cismonica	6.00	0.00	0.00	0.00
Loxospora elatina	0.00	0.00	0.00	0.00
Loxospora ochrophaea	35.0	0.00	55.0	27.5
Micarea botryoides	0.00	0.00	0.00	2.50
Micarea melaena	22.5	4.00	2.50	22.5
Micarea prasina	0.50	25.0	2.50	27.5
Mycoblastus alpinus	1.00	1.00	0.25	0.00
Mycoblastus fucatus	2.75	27.5	2.50	0.75
Mycoblastus sanguinarius	30.0	8.00	27.5	7.50
Parmelia saxatilis	15.5	0.25	11.0	15.5
Parmeliopsis capitata	0.00	0.25	0.25	0.00
Parmeliopsis hyperopta	0.00	0.00	0.00	0.00
Platismatia glauca	23.5	0.75	32.5	1.25
Pseudevernia cladonia	1.00	0.50	1.00	1.00
Pseudevernia consocians	1.50	5.00	5.00	2.00
Ropalospora chlorantha	5.00	0.00	27.5	1.50
Usnea spec.	3.00	0.25	17.5	0.50

Range corresponds with maxima as minima are zero except for: B: *H. physodes*: minimum: 0.50, range: 39.50; DB: *H. physodes*: minimum: 0.50, range: 39.50 and *L. jackii*: minimum: 0.25, range: 34.75.

Tab. 4-A4. Constancy of lichen vegetation on living *Abies balsamea* (B) compared to living *Picea rubens* (R).

	R	B	χ^2	
Species more frequent on B:				
Bryoria capillaris	5.4	35.1	10.1	***
Bryoria furcellata	8.1	24.3	3.58	*
Evernia mesomorpha	0.0	21.6	8.97	**
Flavopunctelia soredica	64.9	83.8	3.47	*
Haematomma ochroleucum	13.5	48.7	10.7	***
Japewia subaurifera	13.5	46.0	9.32	**
Loxospora cismonica	0.0	10.8	4.23	*
Loxospora ochrophaea	0.0	8.1	3.13	*
Mycoblastus fucatus	5.4	29.7	7.56	**
Mycoblastus sanguinarius	37.8	91.9	23.7	***
Parmelia saxatilis	8.1	48.7	15.0	***
Platismatia glauca	35.1	97.3	32.0	***
Pseudevernia cladonia	24.3	64.9	12.3	***
Pseudevernia consocians	10.8	59.5	19.2	***
Ropalospora chlorantha	0.0	13.5	5.36	*
Usnea spec.	16.2	75.7	26.3	***
Species more frequent on R:				
Hypocenomyce friesii	56.8	5.4	22.8	***
Hypocenomyce scalaris	27.0	0.0	11.6	***
Parmeliopsis capitata	8.1	0.0	3.13	*

(Cont.)

(Cont. Tab. 4-A4)

	R	B	χ^2
Indifferent species:			
Alectoria sarmentosa	29.7	29.7	0.00
Arthonia caesia	81.1	78.4	0.08
Bryoria fuscescens	27.0	43.2	2.14
Bryoria nadvornikiana	18.9	8.1	1.85
Bryoria subcana	8.1	21.6	2.67
Bryoria trichodes	2.7	2.7	0.00
Chaenotheca ferruginea	5.4	0.0	0.00
Cladonia coniocraea	37.8	24.3	1.58
Cladonia digitata	5.4	2.7	0.35
Cladonia fimbriata	0.0	2.7	1.01
Cladonia macilenta s.l.	5.4	8.1	0.21
Cladonia pyxidata s.l.	2.7	0.0	1.01
Cladonia squamosa	40.5	35.1	0.23
Hypogymnia krogiae	0.0	2.7	1.01
Hypogymnia physodes	94.6	100	2.06
Hypogymnia tubulosa	0.0	2.7	1.01
Imshaugia aleurites	97.3	97.3	0.00
Lecanora impudens	2.7	8.1	1.06
Lecanora pulicaris	0.0	2.7	1.01
Lepraria jackii	91.9	86.5	0.56
Lecidea nylanderi	81.1	81.1	0.00
Micarea melaena	8.1	8.1	0.00
Micarea prasina	5.4	5.4	0.00

Presence on the investigated trees; n = 37. Statistics: Chi-square test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A5. Constancy of lichen vegetation on dead *Abies balsamea* (DB) compared to dead *Picea rubens* (DR).

	DR	DB	χ^2	
Species more frequent on DB:				
Haematomma ochroleucum	16.2	46.0	7.63	**
Japewia subaurifera	8.1	27.0	4.57	*
Lecidea nylanderi	43.2	75.7	8.07	**
Loxospora ochrophaea	8.1	48.7	15.0	***
Mycoblastus fucatus	10.8	27.0	3.17	*
Mycoblastus sanguinarius	27.0	67.6	12.2	***
Parmelia saxatilis	43.2	78.4	9.58	***
Platismatia glauca	67.6	86.5	3.74	*
Ropalospora chlorantha	2.7	40.5	15.6	***
Usnea spec.	56.8	75.7	2.96	*
Species more frequent on DR:				
Alectoria sarmentosa	48.7	18.9	7.31	**
Arthonia caesia	86.5	54.1	9.32	**
Chaenotheca chrysocephala	13.5	2.7	2.90	*
Cladonia digitata	21.6	5.4	4.16	*
Hypocenomyce friesii	48.7	0.0	23.8	***
Hypocenomyce scalaris	13.5	0.0	5.36	*
Imshaugia aleurites	83.8	48.7	10.2	***
Micarea melaena	37.8	10.8	7.34	**
Micarea prasina	29.7	13.5	2.87	*

(Cont.)

(Cont. Tab. 4-A5)

	DR	DB	χ^2
Indifferent species:			
Bryoria capillaris	24.3	37.8	1.58
Bryoria furcellata	16.2	29.7	1.91
Bryoria fuscescens	46.0	46.0	0.00
Bryoria nadvornikiana	21.6	21.6	0.00
Bryoria subcana	8.1	10.8	0.16
Bryoria trichodes	2.7	0.0	1.01
Chaenotheca ferruginea	5.4	0.0	1.01
Cladonia coniocraea	75.7	78.4	0.08
Cladonia fimbriata	21.6	16.2	0.35
Cladonia macilenta s.l.	13.5	5.4	1.42
Cladonia pyxidata s.l.	13.5	8.1	0.56
Cladonia squamosa	67.6	51.4	2.02
Evernia mesomorpha	24.3	37.8	1.58
Flavopunctelia soredica	86.5	83.8	0.11
Hypogymnia krogiae	5.4	10.8	0.73
Hypogymnia physodes	94.6	100	2.06
Lecanora pulicaris	0.0	2.7	1.01
Lepraria jackii	94.6	100	2.06
Lecidea leprarioides	0.0	5.4	2.06
Micarea botryoides	2.7	0.0	1.01
Mycoblastus alpinus	0.0	2.7	1.01
Parmeliopsis capitata	0.0	2.7	1.01
Pseudevernia cladonia	67.6	56.8	0.92
Pseudevernia consocians	43.2	51.4	0.49

Presence on the investigated trees; n = 37. Statistics: Chi-square test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A6. Mean cover of lichen vegetation on dead (DR) compared to living (R) *Picea rubens*.

	R	DR	
Species more frequent on DR:			
Bryoria capillaris	0.01 ± 0.06	0.07 ± 0.14	*
Chaenotheca chrysocephala	0.00 ± 0.00	0.38 ± 1.49	*
Cladonia coniocraea	1.18 ± 3.66	3.18 ± 5.43	***
Cladonia digitata	0.01 ± 0.06	0.17 ± 0.47	*
Cladonia fimbriata	0.00 ± 0.00	0.24 ± 0.91	**
Cladonia squamosa	0.85 ± 2.41	3.31 ± 6.40	**
Evernia mesomorpha	0.00 ± 0.00	0.06 ± 0.11	**
Flavopunctelia soredica	0.22 ± 0.20	0.35 ± 0.25	*
Micarea melaena	0.19 ± 0.77	1.78 ± 4.39	**
Micarea prasina	0.88 ± 4.26	1.89 ± 5.16	**
Parmelia saxatilis	0.02 ± 0.07	0.95 ± 2.97	***
Platismatia glauca	0.11 ± 0.19	0.28 ± 0.30	**
Pseudevernia cladonia	0.07 ± 0.14	0.28 ± 0.26	***
Pseudevernia consocians	0.15 ± 0.82	0.21 ± 0.38	**
Usnea spec.	0.04 ± 0.09	0.20 ± 0.20	***
Species more frequent on R:			
Lecidea nylanderi	6.86 ± 8.02	2.44 ± 5.11	***

(Cont.)

(Cont. Tab. 4-A6)

	R	DR
Indifferent species:		
Alectoria sarmentosa	0.11 ± 0.19	0.14 ± 0.16
Arthonia caesia	18.1 ± 18.8	18.4 ± 15.3
Bryoria furcellata	0.03 ± 0.12	0.05 ± 0.11
Bryoria fuscescens	0.11 ± 0.20	0.18 ± 0.23
Bryoria nadvornikiana	0.07 ± 0.16	0.05 ± 0.10
Bryoria subcana	0.02 ± 0.07	0.03 ± 0.10
Bryoria trichodes	0.01 ± 0.04	0.01 ± 0.04
Calicium glaucellum	0.00 ± 0.00	0.55 ± 3.29
Chaenotheca ferruginea	0.34 ± 1.68	0.28 ± 1.64
Cladonia macilenta s.l.	0.01 ± 0.06	0.11 ± 0.50
Cladonia pyxidata s.l.	0.01 ± 0.04	0.09 ± 0.41
Haematomma ochroleucum	0.18 ± 0.82	0.81 ± 4.12
Hypocenomyce friesii	2.76 ± 5.51	5.70 ± 9.98
Hypocenomyce scalaris	0.48 ± 1.78	1.11 ± 4.45
Hypogymnia krogiae	0.00 ± 0.00	0.02 ± 0.09
Hypogymnia physodes	2.19 ± 4.05	2.67 ± 4.78
Imshaugia aleurites	5.36 ± 8.83	5.30 ± 8.72
Japewia subaurifera	0.11 ± 0.43	0.02 ± 0.07
Lecanora impudens	0.01 ± 0.04	0.00 ± 0.00
Lepraria jackii	5.27 ± 8.26	3.55 ± 3.91
Loxospora ochrophaea	0.00 ± 0.00	1.39 ± 5.76
Micarea botryoides	0.00 ± 0.00	0.07 ± 0.41
Mycoblastus alpinus	0.05 ± 0.20	0.00 ± 0.00
Mycoblastus fucatus	0.75 ± 4.52	0.05 ± 0.18
Mycoblastus sanguinarius	0.74 ± 1.81	0.51 ± 1.50
Parmeliopsis capitata	0.02 ± 0.07	0.00 ± 0.00
Ropalospora chlorantha	0.00 ± 0.00	0.04 ± 0.25

Arithmetic mean ± standard deviation; calculated from mean values of 2 relevés per tree. n = 37. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A7. Constancy of lichen vegetation on dead (DR) compared to living (R) *Picea rubens*.

	R	DR	χ^2	
Species more frequent DR:				
Alectoria sarmentosa	29.7	48.7	2.78	*
Bryoria capillaris	5.4	24.3	5.23	*
Bryoria fuscescens	27.0	46.0	2.86	*
Chaenotheca chrysocephala	0.0	13.5	5.36	*
Cladonia coniocraea	37.8	75.7	10.8	***
Cladonia digitata	5.4	21.6	4.16	*
Cladonia fimbriata	0.0	21.6	8.97	**
Cladonia pyxidata s.l.	2.7	13.5	2.90	*
Cladonia squamosa	40.5	67.6	5.44	**
Evernia mesomorpha	0.0	24.3	10.3	***
Flavopunctelia soredica	64.9	86.5	4.70	*
Loxospora ochrophaea	0.0	8.1	3.13	*
Micarea melaena	8.1	37.8	9.24	**
Micarea prasina	5.4	29.7	7.56	**
Parmelia saxatilis	8.1	43.2	12.0	***
Platismatia glauca	35.1	67.6	7.79	**
Pseudevernia cladonia	24.3	67.6	13.9	***
Pseudevernia consocians	10.8	43.2	9.87	***
Usnea spec.	16.2	56.8	13.1	***
Species more frequent R:				
Imshaugia aleurites	97.3	83.8	3.95	*
Lecidea nylanderi	81.1	43.2	11.3	***
Parmeliopsis capitata	8.1	0.0	3.13	*

(Cont.)

(Cont. Tab. 4-A7)

	R	DR	χ^2
Indifferent species:			
Arthonia caesia	81.1	86.5	0.40
Bryoria furcellata	8.1	16.2	1.14
Bryoria nadvornikiana	18.9	21.6	0.08
Bryoria subcana	8.1	8.1	0.00
Bryoria trichodes	2.7	2.7	0.00
Chaenotheca ferruginea	5.4	5.4	0.00
Cladonia macilenta s.l.	5.4	13.5	1.42
Haematomma ochroleucum	13.5	16.2	0.11
Hypocenomyce friesii	56.8	48.7	0.49
Hypocenomyce scalaris	27.0	13.5	2.09
Hypogymnia krogiae	0.0	5.4	2.06
Hypogymnia physodes	94.6	94.6	0.00
Japewia subaurifera	13.5	8.1	0.56
Lecanora impudens	2.7	0.0	1.01
Lepraria jackii	91.9	94.6	0.21
Micarea botryoides	0.0	2.7	1.01
Mycoblastus alpinus	5.4	0.0	2.07
Mycoblastus fucatus	5.4	10.8	0.73
Mycoblastus sanguinarius	37.8	27.0	0.84
Ropalospora chlorantha	0.0	2.7	1.01

Presence on the investigated trees; n = 37. Statistics: Chi-square test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A8. Mean cover of lichen vegetation on dead (DB) compared to living (B) *Abies balsamea*.

	B	DB	
Species more frequent on DB:			
Cladonia coniocraea	0.61 ± 1.97	1.05 ± 1.33	***
Cladonia fimbriata	0.01 ± 0.04	0.07 ± 0.19	*
Loxospora ochrophaea	2.12 ± 7.53	5.66 ± 11.0	***
Parmelia saxatilis	1.32 ± 3.22	1.77 ± 2.62	*
Ropalospora chlorantha	0.34 ± 0.16	1.99 ± 5.48	**
Species more frequent on B:			
Arthonia caesia	18.2 ± 22.6	9.46 ± 17.2	*
Imshaugia aleurites	4.58 ± 5.31	0.43 ± 1.08	***
Loxospora cismonica	0.26 ± 1.06	0.00 ± 0.00	*

(Cont.)

(Cont. Tab. 4-A8)

	B	DB
Indifferent species:		
Alectoria sarmentosa	0.09 ± 0.16	0.06 ± 0.14
Bryoria capillaris	0.20 ± 0.35	0.19 ± 0.31
Bryoria furcellata	0.71 ± 3.77	0.13 ± 0.23
Bryoria fuscescens	0.40 ± 0.81	0.31 ± 0.51
Bryoria nadvornikiana	0.03 ± 0.10	0.10 ± 0.25
Bryoria subcana	0.13 ± 0.33	0.03 ± 0.08
Bryoria trichodes	0.01 ± 0.04	0.00 ± 0.00
Chaenotheca chrysocephala	0.00 ± 0.00	0.47 ± 2.88
Cladonia digitata	0.01 ± 0.04	0.05 ± 0.25
Cladonia macilenta s.l.	0.02 ± 0.07	0.03 ± 0.11
Cladonia pyxidata s.l.	0.00 ± 0.00	0.07 ± 0.29
Cladonia squamosa	0.41 ± 1.73	1.34 ± 5.84
Evernia mesomorpha	0.09 ± 0.18	0.12 ± 0.17
Flavopunctelia soredica	0.55 ± 0.45	0.65 ± 1.22
Haematomma ochroleucum	2.25 ± 4.35	4.14 ± 7.96
Hypocenomyce friesii	0.08 ± 0.42	0.00 ± 0.00
Hypogymnia krogiae	0.14 ± 0.82	0.89 ± 3.13
Hypogymnia physodes	12.2 ± 10.1	11.5 ± 9.89
Hypogymnia tubulosa	0.01 ± 0.04	0.00 ± 0.00
Japewia subaurifera	0.43 ± 0.74	0.59 ± 2.52
Lecanora impudens	0.15 ± 0.82	0.00 ± 0.00
Lecanora pulicaris	0.03 ± 0.16	0.01 ± 0.04
Lepraria jackii	4.93 ± 6.63	6.69 ± 7.61
Lecidea leprarioides	0.00 ± 0.00	1.05 ± 6.33
Lecidea nylanderi	9.50 ± 10.5	4.75 ± 5.99
Micarea melaena	0.63 ± 3.70	0.12 ± 0.45
Micarea prasina	0.02 ± 0.09	0.11 ± 0.43
Mycoblastus alpinus	0.06 ± 0.21	0.01 ± 0.04
Mycoblastus fucatus	0.27 ± 0.58	0.17 ± 0.44
Mycoblastus sanguinarius	5.66 ± 7.61	4.30 ± 6.07
Parmeliopsis capitata	0.00 ± 0.00	0.01 ± 0.04
Platismatia glauca	4.13 ± 5.82	3.70 ± 6.22
Pseudevernia cladonia	0.26 ± 0.27	0.22 ± 0.25
Pseudevernia consocians	0.27 ± 0.33	0.39 ± 0.90
Usnea spec.	0.47 ± 0.54	1.26 ± 2.99

Arithmetic mean ± standard deviation; calculated from mean values of 2 relevés per tree. n = 37. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A9. Constancy of lichen vegetation on dead (DB) compared to living (B) *Abies balsamea*.

	B	DB	χ^2	
Species more frequent on DB:				
Cladonia coniocraea	24.3	78.4	21.6	***
Cladonia fimbriata	2.7	16.2	3.95	*
Cladonia pyxidata s.l.	0.0	8.1	3.13	*
Lepraria jackii	86.5	100	5.36	*
Loxospora ochrophaea	8.1	48.7	15.0	***
Parmelia saxatilis	48.7	78.4	7.06	**
Ropalospora chlorantha	13.5	40.5	6.85	**
Species more frequent on B:				
Arthonia caesia	78.4	54.1	4.89	*
Imshaugia aleurites	97.3	48.7	22.2	***
Japewia subaurifera	46.0	27.0	2.86	*
Lecanora impudens	8.1	0.0	3.13	*
Loxospora cismonica	10.8	0.0	4.23	*
Mycoblastus sanguinarius	91.9	67.6	6.77	**
Platismatia glauca	97.3	86.5	2.90	*

(Cont.)

(Cont. Tab. 4-A9)

	B	DB	χ^2
Indifferent species:			
Alectoria sarmentosa	29.7	18.9	1.18
Bryoria capillaris	35.1	37.8	0.06
Bryoria furcellata	24.3	29.7	0.27
Bryoria fuscescens	43.2	46.0	0.06
Bryoria nadvornikiana	8.1	21.6	2.67
Bryoria subcana	21.6	10.8	1.59
Bryoria trichodes	2.7	0.0	1.01
Chaenotheca chrysocephala	0.0	2.7	1.01
Cladonia digitata	2.7	5.4	0.35
Cladonia macilenta s.l.	8.1	5.4	0.21
Cladonia squamosa	35.1	51.4	1.98
Evernia mesomorpha	21.6	37.8	2.33
Flavopunctelia soredica	83.8	83.8	0.00
Haematomma ochroleucum	48.7	46.0	0.05
Hypocenomyce friesii	5.4	0.0	2.06
Hypogymnia krogiae	2.7	10.8	1.93
Hypogymnia physodes	100	100	0.00
Hypogymnia tubulosa	2.7	0.0	1.01
Lecanora pulicaris	2.7	2.7	0.00
Lecidea leprarioides	0.0	5.4	2.06
Lecidea nylanderi	81.1	75.7	0.32
Micarea melaena	8.1	10.8	0.16
Micarea prasina	5.4	13.5	1.42
Mycoblastus alpinus	10.8	2.7	1.93
Mycoblastus fucatus	29.7	27.0	0.07
Parmeliopsis capitata	0.0	2.7	1.01
Pseudevernia cladonia	64.9	56.8	0.51
Pseudevernia consocians	59.5	51.4	0.49
Usnea spec.	75.7	75.7	0.00

Presence on the investigated trees; n = 37. Statistics: Chi-square test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A10. Range and median of element concentration of incident precipitation in 1999 and 2000. n = 6.

	Year	Min.	Max.	**Range**	Median
NH_4^+ [µmol l^{-1}]	1999	0.00	326	**326**	60.0
	2000	0.00	230	**230**	62.6
NO_3^- [µmol l^{-1}]	1999	0.00	16.9	**16.9**	3.68
	2000	0.00	10.1	**10.1**	1.38
P [µmol l^{-1}]	1999	0.00	9.27	**9.27**	4.63
	2000	2.71	31.4	**28.6**	17.9
S [µmol l^{-1}]	1999	0.50	7.92	**7.42**	2.18
	2000	0.31	5.55	**5.24**	1.76
K [µmol l^{-1}]	1999	3.27	62.6	**59.4**	13.9
	2000	3.43	145	**142**	8.12
Na [µmol l^{-1}]	1999	10.2	38.9	**28.8**	18.1
	2000	11.2	25.4	**14.2**	16.8
Ca [µmol l^{-1}]	1999	0.50	14.2	**13.7**	2.02
	2000	1.75	8.88	**7.13**	3.98
Mg [µmol l^{-1}]	1999	0.00	5.31	**5.31**	0.29
	2000	0.00	2.43	**2.43**	0.26
Fe [µmol l^{-1}]	1999	0.00	1.04	**1.04**	0.19
	2000	0.04	1.33	**1.33**	0.62
Mn [µmol l^{-1}]	1999	0.00	1.22	**1.22**	0.05
	2000	0.01	0.92	**0.91**	0.17
Al [µmol l^{-1}]	1999	1.19	7.30	**6.11**	4.15
	2000	0.44	7.74	**7.30**	4.49
Zn [µmol l^{-1}]	1999	0.00	0.44	**0.44**	0.11
	2000	0.14	0.87	**0.73**	0.44
pH	1999	4.02	5.99	**1.97**	4.42
	2000	4.09	4.92	**0.83**	4.41
Conductivity	1999	5.82	54.8	**49.0**	19.9
[µS cm^{-1}]	2000	7.24	40.2	**33.0**	20.9
Precipitation	1999	5.10	140	**135**	26.8
[l m^{-2} $week^{-1}$]	2000	10.2	48.4	**38.2**	28.3

Tab. 4-A11. Spearman correlation matrix for the parameters measured in incident precipitation in 1999.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	0.30**	0.24*													
S	.	0.71***	.												
K	.	.	.	.											
Na	.	0.54***	.	0.55***	.										
Ca	.	0.80***	0.22*	0.52***	.	0.34***									
Mg	.	0.90***	0.22*	0.74***	.	0.54***	0.80***								
Fe	0.42***	0.46***	0.52***	.	0.33**	.	0.43***	0.39**							
Mn	0.29**	0.50***	0.48***	0.38***	.	0.21*	0.56***	0.51***	0.57***						
Al	.	.	.	0.58***	-0.24*	.	.	.	0.57***	0.28**					
Zn	0.34**	0.52***	0.37***	0.31**	.	.	0.47***	0.43***	0.53***	0.58***	.				
Cu	0.25*	.	0.53***	.	.	.	.	.	0.30**	0.23*	0.26*	0.30**			
pH	0.23*	-0.35***	0.29**	-0.68***	.	-0.33**	-0.25*	-0.36***	0.25*	.	.	.	0.31**		
Cond.	.	0.67***	.	0.89***	.	0.55***	0.49***	0.69***	.	0.23*	.	.	-0.21*	-0.83***	
Vol.	.	.	.	.	-0.44***	.	.	.	.	.	-0.21*	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of each 6 incident precipitation samplers. Levels of significance:
* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A12. Spearman correlation matrix for the parameters measured in incident precipitation in 2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	.	.													
S	.	0.46***	.												
K	.	.	.	.											
Na	.	.	.	.	.										
Ca	.	0.38***	.	.	.	.									
Mg	.	0.54***	-0.25*	0.59***	0.33**	0.22*	0.23*								
Fe	.	.	.	.	.	.	.	.							
Mn	.	-0.26*	.	-0.22*	.	.	.	.	.						
Al	.	.	-0.24*	0.28**	.	-0.24*	0.22*	.	.	.					
Zn	0.27**	.	.	.	.	.	.	.	0.28**	0.21*	.				
Cu	.	.	.	.	.	.	.	.	.	.	.	.			
pH	.	-0.53***	0.27**	-0.77***	.	.	.	-0.51***	.	0.28***	-0.36***	.	.		
Cond.	.	0.58***	-0.24*	0.83***	.	.	.	0.66***	.	.	0.37***	.	.	-0.94***	
Vol.	.	.	0.33**	-0.31**	.	.	.	-0.23*	0.31**	.	-0.32**	0.23*	0.23*	0.44***	-0.42***
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of each 6 incident precipitation samplers. Levels of significance:
* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A13. Spearman correlation matrix for the parameters measured in incident precipitation in 1999/2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	0.19*	.													
S	.	0.61***	.												
K	.	0.25***	-0.48***	0.21**											
Na	.	0.26***	-0.18*	0.32***	0.18*										
Ca	.	0.41***	0.51***	0.17*	-0.20**	.									
Mg	.	0.76***	.	0.66***	0.27***	0.41***	0.50***								
Fe	0.24**	.	0.68***	.	-0.18*	.	0.60***	0.26***							
Mn	0.18*	.	0.63***	.	-0.19**	.	0.69***	0.31***	0.71***						
Al	.	.	.	.	.	-0.18*	0.19*	.	0.15*	.					
Zn	0.23**	.	0.76***	.	-0.42***	-0.15*	0.61***	.	0.72***	0.71***	0.15*				
Cu	.	.	0.74***	.	-0.48***	-0.15*	0.48***	.	0.57***	0.59***	.	0.71***			
pH	.	-0.43***	.	-0.71***	.	.	.	-0.44***	.	.	-0.18*	.	.		
Cond.	.	0.61***	.	0.85***	.	0.25***	0.31***	0.67***	.	.	0.16*	.	.	-0.90***	
Vol.	.	.	.	-0.25***	-0.24***	.	.	.	.	.	-0.24***	.	.	0.23**	-0.30***
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of each 6 incident precipitation samplers. Levels of significance:
* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A14. Range (including minimum and maximum) and median of stem flow of living *Abies balsamea* for the years 1999, 2000 and 99/00.

	Year	Min.	Max.	**Range**	Median
NH_4^+ [µmol l^{-1}]	1999	56.5	148	**91.4**	107
	2000	50.3	87.5	**37.2**	62.8
	99/00	61.0	115	**53.7**	81.4
NO_3^- [µmol l^{-1}]	1999	0.57	4.66	**4.09**	1.85
	2000	0.05	0.58	**0.53**	0.09
	99/00	0.31	2.38	**2.07**	1.05
P [µmol l^{-1}]	1999	5.71	15.3	**9.58**	4.10
	2000	17.2	25.0	**7.81**	3.92
	99/00	11.5	18.8	**7.33**	4.01
S [µmol l^{-1}]	1999	15.3	38.2	**22.9**	29.3
	2000	11.8	24.6	**12.8**	16.1
	99/00	13.5	30.0	**16.4**	22.8
K [µmol l^{-1}]	1999	148	505	**356**	396
	2000	110	365	**255**	249
	99/00	129	435	**305**	321
Na [µmol l^{-1}]	1999	37.6	63.7	**26.1**	51.0
	2000	25.1	36.6	**11.5**	29.5
	99/00	31.3	50.1	**18.8**	42.6
Ca [µmol l^{-1}]	1999	64.0	128	**64.3**	94.7
	2000	41.7	95.9	**54.1**	59.8
	99/00	55.7	103	**47.6**	83.5
Mg [µmol l^{-1}]	1999	19.2	50.3	**31.0**	28.0
	2000	12.4	33.1	**20.6**	18.7
	99/00	17.4	36.5	**19.1**	22.4
Fe [µmol l^{-1}]	1999	0.77	2.34	**1.57**	1.70
	2000	1.20	2.39	**1.19**	1.59
	99/00	0.98	2.36	**1.38**	1.62
Mn [µmol l^{-1}]	1999	7.95	31.9	**24.0**	15.8
	2000	4.39	32.3	**27.9**	8.46
	99/00	6.17	32.1	**25.9**	17.3
Al [µmol l^{-1}]	1999	8.00	14.0	**5.97**	10.5
	2000	7.55	11.4	**3.84**	8.40
	99/00	7.84	12.7	**4.84**	9.67
Zn [µmol l^{-1}]	1999	0.56	1.20	**0.64**	0.70
	2000	0.63	1.31	**0.68**	0.72
	99/00	0.59	1.25	**0.66**	0.70
Cu [µmol l^{-1}]	1999	0.33	0.67	**0.34**	0.39
	2000	0.77	0.86	**0.09**	0.80
	99/00	0.56	0.76	**0.20**	0.59
pH	1999	3.73	3.96	**0.23**	3.82
	2000	3.59	4.00	**0.41**	3.88
	99/00	3.87	4.09	**0.22**	4.01
Conductivity [µS cm^{-1}]	1999	81.8	182	**101**	146
	2000	77.1	168	**90.4**	97.6
	99/00	82.0	175	**93.0**	122
Stem flow	1999	0.50	2.10	**1.60**	1.10
[l $tree^{-1}$ $week^{-1}$]	2000	0.10	3.50	**3.40**	1.00
	99/00	0.40	2.80	**2.40**	1.00

Tab. 4-A15. Range (including minimum and maximum) and median of stem flow of dead *Abies balsamea* for the years 1999, 2000 and 99/00.

	Year	Min.	Max.	**Range**	Median
NH_4^+ [µmol l^{-1}]	1999	65.1	308	**243**	93.8
	2000	48.7	81.1	**32.3**	63.9
	99/00	61.0	178	**117**	78.2
NO_3^- [µmol l^{-1}]	1999	1.73	6.43	**4.70**	3.12
	2000	0.07	0.62	**0.55**	0.15
	99/00	0.93	3.39	**2.46**	1.68
P [µmol l^{-1}]	1999	5.68	29.5	**23.9**	8.97
	2000	16.9	21.7	**4.79**	20.2
	99/00	12.5	25.5	**13.0**	14.8
S [µmol l^{-1}]	1999	8.06	15.5	**7.41**	11.0
	2000	2.81	13.4	**10.6**	5.27
	99/00	6.60	14.4	**7.84**	7.76
K [µmol l^{-1}]	1999	120	433	**313**	185
	2000	47.5	327	**280**	117
	99/00	93.4	380	**287**	152
Na [µmol l^{-1}]	1999	23.7	41.6	**18.0**	29.1
	2000	17.8	25.0	**7.12**	19.8
	99/00	21.4	33.3	**11.9**	23.7
Ca [µmol l^{-1}]	1999	40.7	147	**106**	81.2
	2000	15.5	142	**127**	49.0
	99/00	45.2	144	**99.3**	61.9
Mg [µmol l^{-1}]	1999	15.3	49.0	**33.7**	33.7
	2000	5.59	42.1	**36.5**	15.8
	99/00	15.0	45.6	**30.6**	23.2
Fe [µmol l^{-1}]	1999	0.45	0.92	**0.47**	0.63
	2000	0.69	1.20	**0.51**	0.89
	99/00	0.57	1.06	**0.49**	0.74
Mn [µmol l^{-1}]	1999	3.07	25.4	**22.3**	7.07
	2000	0.81	16.6	**15.8**	3.18
	99/00	2.34	21.0	**18.7**	5.36
Al [µmol l^{-1}]	1999	5.56	6.76	**1.20**	6.18
	2000	4.93	6.64	**1.71**	5.46
	99/00	5.29	6.60	**1.31**	5.81
Zn [µmol l^{-1}]	1999	0.41	0.92	**0.51**	0.60
	2000	0.49	1.18	**0.69**	0.65
	99/00	0.46	1.05	**0.59**	0.62
Cu [µmol l^{-1}]	1999	0.30	0.40	**0.10**	0.36
	2000	0.68	0.80	**0.12**	0.72
	99/00	0.50	0.57	**0.07**	0.54
pH	1999	4.09	4.69	**0.60**	4.37
	2000	3.02	4.74	**1.72**	4.26
	99/00	4.34	4.77	**0.43**	4.43
Conductivity [µS cm^{-1}]	1999	53.2	87.5	**34.2**	72.7
	2000	42.3	83.2	**40.9**	52.3
	99/00	48.6	84.4	**35.8**	62.1
Stem flow	1999	0.50	2.10	**1.60**	0.80
[l $tree^{-1}$ $week^{-1}$]	2000	0.20	2.00	**1.80**	0.40
	99/00	0.40	2.10	**1.70**	0.60

Tab. 4-A16. Range (including minimum and maximum) and median of stem flow of living *Picea rubens* for the years 1999, 2000, and 99/00.

	Year	Min.	Max.	**Range**	Median
NH_4^+ [µmol l^{-1}]	1999	60.4	201	**140**	89.0
	2000	42.7	79.3	**36.5**	59.9
	99/00	56.8	140	**83.1**	72.0
NO_3^- [µmol l^{-1}]	1999	2.03	42.5	**40.4**	8.69
	2000	0.12	3.74	**3.62**	0.28
	99/00	1.11	23.1	**22.0**	4.47
P [µmol l^{-1}]	1999	4.66	8.36	**3.70**	5.79
	2000	17.8	20.3	**2.51**	19.1
	99/00	11.7	14.1	**2.42**	12.7
S [µmol l^{-1}]	1999	9.70	34.4	**24.7**	17.2
	2000	7.37	16.3	**8.95**	14.2
	99/00	8.94	25.3	**16.3**	15.8
K [µmol l^{-1}]	1999	72.4	208	**136**	101
	2000	50.0	123	**73.1**	90.8
	99/00	69.9	166	**95.7**	95.8
Na [µmol l^{-1}]	1999	30.6	46.7	**16.1**	38.6
	2000	23.7	31.4	**7.67**	28.4
	99/00	27.5	39.0	**11.5**	33.8
Ca [µmol l^{-1}]	1999	33.9	180	**146**	112
	2000	51.6	112	**60.8**	71.4
	99/00	44.7	126	**80.9**	101
Mg [µmol l^{-1}]	1999	7.74	53.2	**45.5**	28.1
	2000	10.2	28.6	**18.4**	17.1
	99/00	8.99	37.1	**28.1**	23.7
Fe [µmol l^{-1}]	1999	0.60	2.12	**1.52**	1.43
	2000	1.34	1.91	**0.57**	1.77
	99/00	1.04	1.96	**0.92**	1.65
Mn [µmol l^{-1}]	1999	5.02	22.8	**17.8**	14.1
	2000	4.18	17.3	**13.1**	9.69
	99/00	5.06	16.8	**11.7**	13.1
Al [µmol l^{-1}]	1999	5.95	10.1	**4.11**	8.27
	2000	6.45	7.91	**1.46**	6.92
	99/00	6.22	8.57	**2.35**	7.71
Zn [µmol l^{-1}]	1999	0.37	2.76	**2.39**	0.70
	2000	0.65	1.63	**0.98**	0.84
	99/00	0.54	2.20	**1.66**	0.80
Cu [µmol l^{-1}]	1999	0.33	0.42	**0.09**	0.37
	2000	0.62	0.72	**0.10**	0.69
	99/00	0.49	0.55	**0.06**	0.53
pH	1999	3.58	3.94	**0.36**	3.74
	2000	3.68	4.11	**0.43**	3.85
	99/00	3.76	4.03	**0.27**	3.84
Conductivity [µS cm^{-1}]	1999	66.1	176	**110**	107
	2000	56.6	112	**55.3**	90.2
	99/00	64.4	136	**71.6**	97.9
Stem flow	1999	0.50	2.60	**2.10**	1.40
[l $tree^{-1}$ $week^{-1}$]	2000	0.50	3.30	**2.80**	1.40
	99/00	0.70	3.00	**2.30**	1.40

Tab. 4-A17. Range (including minimum and maximum) and median of stem flow of dead *Picea rubens* for the years 1999, 2000 and 99/00.

	Year	Min.	Max.	**Range**	Median
NH_4^+ [µmol l^{-1}]	1999	61.0	165	**104**	94.3
	2000	43.4	86.0	**42.6**	61.6
	99/00	52.2	117	**64.9**	81.7
NO_3^- [µmol l^{-1}]	1999	2.72	8.30	**5.58**	5.09
	2000	0.04	0.76	**0.72**	0.21
	99/00	1.54	4.29	**2.75**	2.76
P [µmol l^{-1}]	1999	4.92	18.2	**13.3**	7.19
	2000	17.6	22.1	**4.46**	19.9
	99/00	11.6	20.1	**8.52**	13.4
S [µmol l^{-1}]	1999	6.59	14.6	**7.99**	11.8
	2000	3.61	11.3	**7.64**	7.93
	99/00	5.10	12.1	**6.98**	10.2
K [µmol l^{-1}]	1999	51.6	558	**506**	165
	2000	37.7	279	**241**	99.2
	99/00	44.6	419	**374**	126
Na [µmol l^{-1}]	1999	25.9	36.5	**10.6**	29.8
	2000	18.6	23.3	**4.74**	21.1
	99/00	22.2	29.1	**6.85**	26.3
Ca [µmol l^{-1}]	1999	39.0	190	**151**	101
	2000	18.7	248	**229**	96.6
	99/00	28.9	219	**190**	91.9
Mg [µmol l^{-1}]	1999	8.40	35.6	**27.2**	23.3
	2000	4.33	41.8	**37.4**	22.8
	99/00	6.36	38.6	**32.3**	24.4
Fe [µmol l^{-1}]	1999	0.30	0.92	**0.62**	0.72
	2000	0.61	1.49	**0.88**	1.06
	99/00	0.46	1.18	**0.72**	0.91
Mn [µmol l^{-1}]	1999	4.32	14.6	**10.3**	10.0
	2000	1.77	18.9	**17.1**	9.65
	99/00	3.04	16.1	**13.1**	10.7
Al [µmol l^{-1}]	1999	5.67	7.72	**2.05**	6.80
	2000	4.85	7.19	**2.34**	6.55
	99/00	5.26	7.22	**1.96**	6.68
Zn [µmol l^{-1}]	1999	0.29	0.99	**0.70**	0.68
	2000	0.54	1.91	**1.37**	0.90
	99/00	0.42	1.35	**0.93**	0.79
Cu [µmol l^{-1}]	1999	0.29	0.45	**0.16**	0.35
	2000	0.63	0.79	**0.16**	0.72
	99/00	0.51	0.59	**0.08**	0.53
pH	1999	4.00	4.45	**0.45**	4.20
	2000	4.01	4.49	**0.48**	4.26
	99/00	4.11	4.65	**0.54**	4.29
Conductivity [µS cm^{-1}]	1999	44.3	100	**55.8**	75.4
	2000	32.5	89.6	**57.1**	65.2
	99/00	38.4	79.8	**41.4**	74.4
Stem flow	1999	0.70	1.90	**1.20**	1.10
[l $tree^{-1}$ $week^{-1}$]	2000	0.50	2.30	**1.80**	1.20
	99/00	0.60	2.10	**1.50**	1.10

Tab. 4-A18. Bivariate analysis of variance for the influence of the variables 'tree species' (B, R), 'tree vitality' (dead, living), and 'tree species and tree vitality' on the chemical composition of the stem flow (measuring period 1999).

	Total		Tree species (df=1)		Tree vitality (df=1)		Tree species × Tree vitality (df=1)	
	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value
NH_4^+	7	0.9	3	1.1	2	0.6	2	0.8
NO_3^-	41	8.0 ***	21	12.7 **	8	4.8 *	11	6.7 *
P	20	2.9 *	13	5.6 *	7	10.0	0	0.0
S	63	19.5 ***	7	6.8 *	46	42.8 ***	9	8.9 **
K	39	7.4 ***	28	15.9 ***	1	0.4	10	5.7 *
Na	63	19.8 ***	7	6.3 *	47	44.3 ***	9	8.6 **
Ca	5	0.6	4	1.6	0	0.1	0	0.0
Mg	8	1.0	7	2.9	0	0.1	0	0.1
Fe	68	25.3 ***	1	0.9	65	71.7 ***	3	3.2
Mn	25	3.9 *	2	0.9	20	9.2 **	4	1.7
Al	75	35.8 ***	4	6.2 *	55	78.3 ***	16	22.7 ***
Zn	10	1.3	1	0.6	7	2.8	1	0.4
Cu	20	3.0 *	4	1.7	10	4.5 *	6	2.8
pH	74	32.9 ***	14	18.2 ***	60	80.4 ***	0	0.0
Cond.	58	16.1 ***	2	1.9	52	42.9 ***	4	3.4
Vol.	14	1.9	8	3.1	6	2.4	0	0.0

Tab. 4-A19. Bivariate analysis of variance for the influence of the variables ‚tree species' (B, R), ‚tree vitality' (dead, living), and ‚tree species and tree vitality' on the chemical composition of the stem flow (measuring period 2000).

	Total		Tree species (df=1)		Tree vitality (df=1)		Tree species × Tree vitality (df=1)	
	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value
NH_4^+	2	0.2	2	0.6	0	0.1	0	0.1
NO_3^-	15	2.1	7	2.7	4	1.5	5	2.2
P	10	1.2	7	2.5	1	0.3	2	0.9
S	66	22.9 ***	0	0.3	60	62.0 ***	6	6.3 *
K	35	6.4 **	21	11.4 **	1	0.7	13	7.1 *
Na	72	30.1 ***	0	0.2	70	87.1 ***	2	2.9
Ca	17	2.5	13	5.3 *	1	0.3	4	1.8
Mg	4	0.5	0	0.2	1	0.2	3	1.1
Fe	68	24.7 ***	0	0.4	66	71.7 ***	2	1.8
Mn	22	3.2 *	2	0.8	11	5.0 *	9	3.9
Al	70	27.5 ***	2	2.4	46	53.8 ***	22	26.4 ***
Zn	13	1.8	11	4.5 *	0	0.0	1	0.8
Cu	63	19.5 ***	29	27.2 ***	4	3.3	30	28.0 ***
pH	78	41.6 ***	5	8.5 **	71	113.7 ***	2	2.5
Cond.	57	15.3 ***	0	0.1	51	41.1 ***	6	4.7 *
Vol.	21	3.1 *	11	5.1 *	9	4.2 *	0	0.2

Tab. 4-A20. Bivariate analysis of variance for the influence of the variables ‚tree species' (B, R), ‚tree vitality' (dead, living), and ‚tree species and tree vitality' on the chemical composition of the stem flow (measuring period 1999/2000).

	Total		Tree species (df=1)		Tree vitality (df=1)		Tree species × Tree vitality (df=1)	
	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value
NH_4^+	7	0.8	4	1.3	1	0.5	2	0.7
NO_3^-	40	7.7 ***	21	12.0 **	8	4.6 *	11	6.5 *
P	20	3.0 *	14	6.2 *	6	2.7	0	0.0
S	68	25.1 ***	4	4.2 *	56	61.4 ***	9	9.8 **
K	40	7.7 ***	27	15.5 ***	1	0.6	12	6.9 *
Na	68	24.4 ***	4	3.9	57	62.1 ***	7	7.1 *
Ca	12	1.6	10	4.1	0	0.0	2	0.8
Mg	2	0.3	2	0.7	0	0.0	0	0.2
Fe	71	28.1 ***	0	0.1	68	81.5 ***	2	2.9
Mn	25	4.0 *	0	0.0	18	8.6 **	7	3.3
Al	77	38.9 ***	3	5.2 *	54	81.9 ***	20	29.6 ***
Zn	8	1.0	6	2.2	2	0.9	0	0.0
Cu	52	12.7 ***	19	14.3 ***	9	6.4 *	24	17.6 ***
pH	82	52.0 ***	11	20.3 ***	71	135.1 ***	0	0.6
Cond.	63	20.1 ***	1	1.1	57	54.0 ***	5	5.1 *
Vol.	19	2.7	10	4.4 *	8	3.6	0	0.1

Tab. 4-A21. Spearman correlation matrix for the parameters measured in stem flow of living *Picea rubens* in 1999.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	.	.													
S	.	.	.												
K	.	0.81**	.	0.85**											
Na	.	.	.	0.96***	0.78**										
Ca	.	0.65*	.	0.94***	0.82**	0.89***									
Mg	.	.	.	0.98***	0.79**	0.98***	0.87**								
Fe	.	.	.	0.95***	0.77**	0.95***	0.94***	0.93***							
Mn	.	.	.	0.83**	.	0.89***	0.76*	0.90***	0.87**						
Al	.	.	.	0.96***	0.75*	0.96***	0.95***	0.94***	0.99***	0.88***					
Zn	.	.	.	.	0.65*	.	.	.	.	.	.				
Cu	.	.	.	.	.	.	.	.	.	.	.	.			
pH	.	.	.	-0.71*	.	.	.	-0.67*	-0.66*	.	-0.70*	.	.		
Cond.	.	.	.	0.95***	0.78**	0.89***	0.92***	0.90***	0.90***	0.76*	0.94***	.	.	-0.81**	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A22. Spearman correlation matrix for the parameters measured in stem flow of living *Picea rubens* in 2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	.	.													
S	.	.	.												
K	.	0.79**	.	.											
Na	.	.	.	0.98***	.										
Ca	.	.	.	0.87**	.	0.79**									
Mg	.	.	.	0.88***	.	0.85**	0.92***								
Fe	.	.	.	.	.	.	0.73*	0.71*							
Mn	.	.	.	0.70*	.	.	0.90***	0.79**	0.82**						
Al	.	.	.	.	0.66*	0.65*	0.68*	0.78**	.	.					
Zn	.	.	.	.	.	.	.	.	.	.	.				
Cu	.	.	.	.	.	.	.	.	.	.	0.66*	.			
pH	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cond.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A23. Spearman correlation matrix for the parameters measured in stem flow of living *Picea rubens* in 1999/2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	0.78**	.													
S	.	.	.												
K	.	0.89***	.	0.83**											
Na	.	.	0.66*	0.96***	0.73*										
Ca	.	.	.	0.87**	0.78**	0.85**									
Mg	.	.	.	0.84**	0.68*	0.81**	0.93***								
Fe	.	.	.	0.74*	.	0.78**	0.79**	0.77**							
Mn	.	.	.	.	.	.	0.76*	0.73*	0.65*						
Al	.	.	.	0.81**	0.75*	0.79**	0.88***	0.76*	0.92***	0.64*					
Zn	.	.	.	.	.	.	.	.	.	.	.				
Cu	.	.	.	.	.	.	.	.	.	.	.	.			
pH	.	.	.	.	.	-0.72*	.	.	-0.75*	.	-0.65*	.	.		
Cond.	.	.	.	0.95***	0.73*	0.94***	0.77**	0.77**	0.84**	.	0.83**	.	.	-0.81**	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A24. Spearman correlation matrix for the parameters measured in stem flow of dead *Picea rubens* in 1999.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	0.94***	.													
S	.	.	.												
K	0.82**	.	0.78**	.											
Na	0.73*	.	0.85**	.	0.73*										
Ca	.	.	.	0.67*	.	.									
Mg	.	.	.	0.85**	.	.	0.65*								
Fe	.	.	.	.	.	.	.	.							
Mn	.	.	.	0.71*	.	.	.	.	.						
Al	.	.	.	.	.	.	.	.	.	.					
Zn	.	.	.	0.68*	.	.	0.99***	0.71*	.	0.64*	.				
Cu	.	.	.	.	.	.	.	.	.	.	.	.			
pH	.	.	.	.	0.76*	.	.	.	.	.	.	.	.		
Cond.	0.70*	.	.	0.88***	0.72*	.	.	0.78**	.	0.68*	0.66*	.	.	.	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A25. Spearman correlation matrix for the parameters measured in stem flow of dead *Picea rubens* in 2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	.	.													
S	.	.	0.75*												
K	.	.	.	.											
Na	.	.	.	0.73*	.										
Ca	.	.	0.64*	0.76*	.	0.83									
Mg	.	.	.	0.84**	.	0.73*	0.78**								
Fe	.	.	.	.	0.75*	.	.	0.71*							
Mn	.	.	.	0.94***	.	0.83**	0.84**	0.93***	.						
Al	.	.	.	0.71*	0.71*	.	.	0.76*	0.76*	0.70*					
Zn	.	.	0.66*	0.66*	.	.	0.87**	0.79**	.	0.77**	.				
Cu	.	.	.	.	.	.	.	.	.	.	.	.			
pH	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cond.	.	.	.	0.92***	.	.	0.65*	0.88***	.	0.93***	0.73*	0.67*	.	.	
Vol.	0.84**	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A26. Spearman correlation matrix for the parameters measured in stem flow of dead *Picea rubens* in 1999/2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	0.76*	.													
S	.	.	.												
K	0.65*	.	0.72*	.											
Na	.	.	0.67*	.	.										
Ca	.	.	.	0.68*	.	.									
Mg	.	.	.	0.82**	.	.	0.67*								
Fe	.	.	.	.	0.72*	.	.	.							
Mn	.	.	.	0.90***	.	0.72*	0.70*	0.73*	.						
Al	0.68*	.	0.75*	.	0.75*	.	.	.	0.65*	.					
Zn	.	.	.	0.71*	.	.	0.96***	0.73*	.	0.70*	.				
Cu	.	.	.	.	.	.	.	.	.	.	.	.			
pH	.	.	.	.	0.77**	.	.	.	.	.	.	.	.		
Cond.	.	.	.	0.79**	.	0.66*	.	0.76*	.	0.84**	.	.	.	.	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A27. Spearman correlation matrix for the parameters measured in stem flow of living *Abies balsamea* in 1999.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	0.80**														
P	.	.													
S	.	.	.												
K	.	.	.	0.70*											
Na	.	.	.	0.93***	.										
Ca	.	.	0.83**	0.90***	.	0.77*									
Mg	.	.	0.70*	0.93***	.	0.80**	0.93***								
Fe	.	.	0.82**	.	0.83**	.	.	.							
Mn	.	.	.	0.70*	0.70*	.	.	0.72*	.						
Al	.	.	.	.	.	0.73*	.	.	.	.					
Zn	.	.	.	0.83**	0.73*	0.70*	0.75*	0.82**	.	0.93***	.				
Cu	.	.	0.78*	0.73*	.	0.67*	0.77*	0.67*	0.68*	0.75*	.	0.82**			
pH	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cond.	.	.	.	.	0.70*	0.93***	0.90***	0.93***	.	0.70*	.	0.83**	0.73*	.	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A28. Spearman correlation matrix for the parameters measured in stem flow of living *Abies balsamea* in 2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	.	.													
S	0.73*	.	0.87**												
K	.	.	.	0.87**											
Na	.	.	.	0.77*	0.73*										
Ca	.	.	.	0.70*	.	.									
Mg	0.73*	.	.	0.75*	0.80**	.	0.92***								
Fe	0.75*	.	.	0.93***	0.85**	.	0.78*	0.80**							
Mn	.	.	.	.	.	.	0.78*	0.82**	.						
Al	.	.	.	0.93***	0.78*	.	0.73*	0.72*	0.92***	.					
Zn	.	.	.	0.70*	0.70*	.	0.93***	0.92***	0.70*	0.90***	0.70*				
Cu	.	.	0.78*	.	.	.	.	.	.	.	.	0.73*			
pH	.	.	.	.	.	.	.	.	.	.	-0.68*	.	.		
Cond.	.	-0.68*	.	.	.	0.72*	.	0.70*	.	.	.	.	.	.	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A29. Spearman correlation matrix for the parameters measured in stem flow of living *Abies balsamea* in 1999/2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	0.80**														
P	.	.													
S	.	.	.												
K	.	.	.	0.73*											
Na	.	.	.	0.97***	0.67*										
Ca	.	.	.	0.87**	0.68*	0.78*									
Mg	.	.	.	0.78*	.	0.67*	0.80**								
Fe	.	.	.	0.70*	0.85**	.	0.75*	0.70*							
Mn	.	.	.	0.77*	.	0.70*	0.77*	0.68*	.						
Al	.	.	.	0.68*	0.72*	0.72*	.	.	0.73*	.					
Zn	.	.	.	0.90**	.	0.81**	0.88**	0.74*	.	0.90**	.				
Cu	.	.	0.73*	.	.	.	.	.	0.68*	.	.	0.81**			
pH	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cond.	.	.	.	0.92***	.	0.92***	0.82**	0.83**	.	0.77*	.	0.80**	.	.	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A30. Spearman correlation matrix for the parameters measured in stem flow of dead *Abies balsamea* in 1999.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	0.78**	.													
S	0.65*	.	0.84**												
K	.	.	.	.											
Na	0.79**	.	0.90***	0.88***	.										
Ca	.	.	.	0.87**	.	.									
Mg	.	.	.	0.70*	.	.	0.71*								
Fe	.	.	.	.	.	.	.	.							
Mn	0.83**	.	0.75*	0.85**	.	0.81**	0.66*	.	.						
Al	.	.	.	.	.	.	.	.	0.78**	.					
Zn	.	.	.	0.77**	.	0.73*	0.71*	.	.	0.84**	.				
Cu	0.66*	.	.	.	.	.	.	.	.	.	.	.			
pH	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cond.	.	.	0.72*	0.70*	.	0.73*	.	0.63*	.	.	.	0.73*	.	.	
Vol.	.	.	.	.	.	.	.	.	.	.	0.63*	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A31. Spearman correlation matrix for the parameters measured in stem flow of dead *Abies balsamea* in 2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	0.73*	.													
S	.	.	0.66*												
K	.	.	.	0.67*											
Na	.	.	.	0.78**	.										
Ca	.	.	.	.	0.66*	0.64*									
Mg	.	.	0.68*	0.81**	0.90***	.	0.75*								
Fe	.	.	.	.	0.87**	.	.	0.85**							
Mn	.	.	.	0.87**	.	0.78**	.	.	.						
Al	.	.	.	0.76*	0.67*	.	.	0.82**	0.77**	.					
Zn	.	.	0.67*	0.99***	0.76*	0.75*	0.68*	0.87**	0.68*	0.79**	0.77**				
Cu	.	.	0.64*	.	.	.	.	0.71*	.	.	.	.			
pH	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cond.	.	.	.	0.88***	.	0.71*	.	.	.	0.70*	0.70*	0.85**	.	.	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coefficients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A32. Spearman correlation matrix for the parameters measured in stem flow of dead *Abies balsamea* in 1999/2000.

	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.
NO_3^-	.														
P	0.76*	.													
S	0.75*	.	0.94***												
K	.	.	.	.											
Na	0.90***	.	0.92***	0.95***	.										
Ca	.	.	.	0.74*	.	0.66*									
Mg	.	.	.	.	.	.	.								
Fe	.	.	.	.	0.65*	.	.	.							
Mn	0.82**	.	0.87**	0.88***	.	0.94***	0.65*	.	.						
Al	.	.	.	0.67*	.	.	.	.	0.70*	.					
Zn	0.74*	.	0.91***	0.99***	.	0.92***	0.77**	0.64*	.	0.84**	0.74*				
Cu	.	.	.	.	.	.	.	.	.	.	.	.			
pH	.	.	.	.	0.67*	.	.	.	.	.	.	.	.		
Cond.	.	.	0.78**	0.87***	.	0.76*	0.76*	0.79**	.	0.68*	0.78**	0.92***	.	.	
Vol.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	NH_4^+	NO_3^-	P	S	K	Na	Ca	Mg	Fe	Mn	Al	Zn	Cu	pH	Cond.

Correlation coeffcients are calculated from weekly mean values of the 10 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A33. Spearman correlation between stem flow and incident precipitation at living (R) and dead (DR) *Picea rubens* as well as living (B) and dead (DB) *Abies balsamea*.

		R	DR	B	DB
NH_4^+	1999	-	-	0.57 *	-
	2000	0.64 **	-	0.57 *	0.56 *
NO_3^-	1999	0.57 *	0.58 *	0.59 *	0.69 **
	2000	-	0.57 *	-	0.50 *
P	1999	-	-	0.74 **	-
	2000	-	-	0.71 **	-
S	1999	0.78 ***	-	0.75 **	-
	2000	-	-	-	-
Na	1999	-	-	0.66 **	0.69 **
	2000	0.64 **	-	-	0.71 **
Mg	1999	0.72 **	-	-	-
	2000	-	-	-	-
Fe	1999	-	-	-	-
	2000	-	-	0.61 *	0.64 **
Zn	1999	0.53 *	-	-	-
	2000	-	-	-	-
Cu	1999	-	-	-	-
	2000	-	-	0.67 **	0.54 *
pH	1999	0.76 ***	0.66 **	0.84 ***	0.86 ***
	2000	-	-	-	0.58 *
Cond.	1999	0.54 *	-	-	-
	2000	-	-	-	-
Volume	1999	0.74 **	0.70 **	0.63 *	0.70 **
	2000	0.57 *	0.85 ***	0.62 *	0.85 ***

Numbers represent weekly mean values of 10 trees per type of tree and per year as well as 6 rain samplers.

Tab. 4-A34. Dispersal of the data from bark analyses of living *Picea rubens*. n = 27.

	Coefficient of variation [%]	Min.	Max.	**Range**	Median
N [µmol g^{-1}]	23.9	181	423	**242**	220
C [mmol g^{-1}]	4.71	38.1	47.5	**9.37**	40.7
K [µmol g^{-1}]	114	2.76	45.1	**42.4**	5.47
Ca [µmol g^{-1}]	30.7	75.4	276	**201**	157
Mg [µmol g^{-1}]	29.6	2.56	7.47	**4.91**	4.12
Fe [µmol g^{-1}]	43.8	0.61	3.65	**3.04**	1.48
Mn [µmol g^{-1}]	41.0	3.53	13.7	**10.1**	6.44
Zn [µmol g^{-1}]	43.1	0.42	2.34	**1.92**	0.78
Pb [µmol g^{-1}]	253	0.00	0.14	**0.14**	0.00
Cu [µmol g^{-1}]	25.3	0.04	0.11	**0.07**	0.06
pH (H_2O)	5.65	3.08	4.04	**0.96**	3.43
pH (KCl)	4.81	2.78	3.51	**0.73**	3.05
Conductivity [µS cm^{-1}]	28.7	64.0	286	**222**	157

Tab. 4-A35. Dispersal of the data from bark analyses of dead *Picea rubens*. n = 27.

	Coefficient of variation [%]	Min.	Max.	**Range**	Median
N [µmol g^{-1}]	14.1	157	314	**157**	220
C [mmol g^{-1}]	2.58	38.4	42.9	**4.42**	39.9
K [µmol g^{-1}]	47.6	4.60	28.0	**23.4**	8.88
Ca [µmol g^{-1}]	29.7	106	303	**197**	183
Mg [µmol g^{-1}]	53.3	3.45	25.1	**22.1**	7.03
Fe [µmol g^{-1}]	37.8	0.44	2.18	**1.74**	1.47
Mn [µmol g^{-1}]	29.7	3.29	12.9	**9.58**	8.04
Zn [µmol g^{-1}]	29.1	0.56	1.80	**1.24**	1.10
Pb [µmol g^{-1}]	363	0.00	0.08	**0.08**	0.00
Cu [µmol g^{-1}]	21.6	0.03	0.08	**0.05**	0.05
pH (H_2O)	4.44	3.26	3.93	**0.67**	3.59
pH (KCl)	4.75	2.95	3.54	**0.59**	3.16
Conductivity [µS cm^{-1}]	24.5	104	278	**174**	160

Tab. 4-A36. Dispersal of the data from bark analyses in living *Abies balsamea*. n =27.

	Coefficient of variation [%]	Min.	Max.	**Range**	Median
N [µmol g^{-1}]	16.60	232	551	**319**	362
C [mmol g^{-1}]	3.72	41.0	48.0	**7.07**	44.2
K [µmol g^{-1}]	46.20	5.09	75.9	**70.8**	36.8
Ca [µmol g^{-1}]	21.82	58.2	198	**140**	133
Mg [µmol g^{-1}]	31.43	3.04	15.1	**12.0**	9.78
Fe [µmol g^{-1}]	68.39	0.50	4.68	**4.18**	0.99
Mn [µmol g^{-1}]	73.63	5.29	104	**98.4**	21.7
Zn [µmol g^{-1}]	37.69	0.47	2.06	**1.59**	1.05
Pb [µmol g^{-1}]	519.62	0.00	0.06	**0.06**	0.00
Cu [µmol g^{-1}]	19.58	0.05	0.15	**0.10**	0.12
pH (H_2O)	6.16	3.30	4.46	**1.16**	3.98
pH (KCl)	6.51	3.01	3.96	**0.95**	3.53
Conductivity [µS cm^{-1}]	20.94	123	278	**155**	193

Tab. 4-A37. Dispersal of the data from bark analyses in dead *Abies balsamea*. n = 27.

	Coefficient of variation [%]	Min.	Max.	**Range**	Median
N [µmol g^{-1}]	17.3	328	630	**302**	456
C [mmol g^{-1}]	4.08	39.1	46.7	**7.57**	42.4
K [µmol g^{-1}]	50.5	6.21	57.3	**51.1**	25.1
Ca [µmol g^{-1}]	27.6	105	307	**202**	179
Mg [µmol g^{-1}]	48.7	2.26	28.4	**26.1**	16.1
Fe [µmol g^{-1}]	44.1	0.60	2.62	**2.02**	1.02
Mn [µmol g^{-1}]	75.3	4.36	63.7	**59.3**	14.3
Zn [µmol g^{-1}]	36.0	0.67	2.56	**1.89**	1.20
Pb [µmol g^{-1}]	362	0.00	0.12	**0.12**	0.00
Cu [µmol g^{-1}]	26.7	0.05	0.18	**0.13**	0.11
pH (H_2O)	6.23	3.48	4.79	**1.31**	4.06
pH (KCl)	10.0	2.58	4.41	**1.83**	3.62
Conductivity [µS cm^{-1}]	29.7	65.0	256	**191**	154

Tab. 4-A38. Bivariate analysis of variance for the influence of the variables 'tree species' (B, R), 'tree vitality' (dead, living), and 'tree species and tree vitality' on the chemical composition of the bark.

	Total		Tree species (df=1)		Tree vitality (df=1)		Tree species × Tree vitality (df=1)	
	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value
N	75	103.1 ***	66	271.0 ***	3	13.2 ***	6	25.0 ***
C	50	34.6 ***	41	85.2 ***	8	16.9 ***	1	1.9
K	54	40.9 ***	48	107.8 ***	2	3.6	5	11.4 **
Ca	18	7.8 ***	2	2.9	15	19.6 ***	1	0.9
Mg	40	23.2 ***	24	41.2 ***	16	27.9 ***	0	0.4
Fe	5	1.8	4	4.8 *	0	0.0	1	0.6
Mn	33	17.1 ***	28	42.9 ***	2	3.0	4	5.5 *
Zn	10	3.8 *	6	7.0 **	4	4.4 *	0	0.1
Pb	3	1.1	1	0.9	0	0.1	2	2.2
Cu	65	65.4 ***	64	192.9 ***	1	3.3	0	0.1
pH (H_2O)	62	57.5 ***	59	161.8 ***	4	10.6 **	0	0.0
pH (KCl)	46	29.0 ***	43	82.2 ***	3	4.8 *	0	0.1
Cond.	6	2.0	0	0.0	2	2.7	3	3.4

Tab. 4-A39. Range (including minimum and maximum) and median of element contents of extractions with H_2O, EDTA, and $SrCl_2$ as well as of total bark content of *Abies balsamea*. n = 20.

	Min.	Max.	**Range**	Median
H_2O eluate:				
K	2.79	29.5	**26.7**	16.0
Mg	0.66	4.15	**3.49**	1.62
Ca	1.17	9.16	**7.99**	2.76
Zn	0.02	0.18	**0.16**	0.07
Cu	0.02	0.03	**0.01**	0.02
Mn	0.15	7.34	**7.19**	1.21
Fe	0.02	0.04	**0.02**	0.02
EDTA extract:				
K	4.04	45.1	**41.1**	22.9
Mg	2.59	10.2	**7.57**	4.83
Ca	9.11	77.8	**68.7**	28.0
Zn	0.58	2.16	**1.58**	1.07
Cu	0.05	0.11	**0.06**	0.07
Mn	3.39	56.8	**53.4**	21.5
Fe	0.30	1.39	**1.09**	0.50
$SrCl_2$ extract:				
K	5.35	50.9	**45.6**	25.3
Mg	4.52	27.2	**22.7**	8.14
Ca	22.0	92.0	**70.0**	44.5
Zn	0.26	0.67	**0.41**	0.41
Cu	0.00	0.03	**0.03**	0.02
Mn	2.97	36.2	**33.2**	11.3
Fe	0.00	0.04	**0.04**	0.02
Total content:				
K	5.53	74.1	**68.5**	34.0
Mg	8.65	40.0	**31.3**	12.2
Ca	76.4	211	**135**	113
Zn	0.69	1.93	**1.24**	1.19
Cu	0.09	0.39	**0.30**	0.27
Mn	4.44	57.6	**53.1**	19.8
Fe	0.59	2.47	**1.88**	1.09

Tab. 4-A40. Range (including minimum and maximum) and median of element contents of extractions with H_2O, EDTA, and $SrCl_2$ as well as of total bark content of *Picea rubens*. n = 20.

	Min.	Max.	**Range**	Median
H_2O eluate:				
K	1.69	24.0	**22.3**	2.49
Mg	0.33	1.85	**1.52**	0.53
Ca	1.80	7.78	**5.98**	3.44
Zn	0.02	0.14	**0.12**	0.04
Cu	0.00	0.02	**0.02**	0.02
Mn	0.15	0.95	**0.80**	0.38
Fe	0.02	0.04	**0.02**	0.02
EDTA extract:				
K	2.51	40.4	**37.9**	3.95
Mg	0.95	6.62	**5.67**	2.18
Ca	12.4	51.2	**38.8**	22.5
Zn	0.31	6.96	**6.65**	0.86
Cu	0.03	0.09	**0.06**	0.05
Mn	1.60	10.0	**8.43**	5.01
Fe	0.17	1.49	**1.32**	0.44
$SrCl_2$ extract:				
K	2.71	51.5	**48.8**	4.50
Mg	1.36	12.2	**10.9**	3.70
Ca	27.2	77.5	**50.3**	52.4
Zn	0.21	3.78	**3.57**	0.44
Cu	0.02	0.02	**0.00**	0.02
Mn	1.49	7.79	**6.30**	4.08
Fe	0.02	0.06	**0.04**	0.04
Total content:				
K	2.24	58.2	**56.0**	7.23
Mg	3.94	18.3	**14.4**	7.23
Ca	37.6	336	**298**	130
Zn	0.46	7.82	**7.36**	1.07
Cu	0.11	0.35	**0.24**	0.19
Mn	2.77	11.5	**8.73**	6.09
Fe	0.54	4.01	**3.47**	1.11

Tab. 4-A41. Percentage values of extracted concentrations related to the mean of total bark content in [mmol kg^{-1} DW] from the corresponding element.

	A. balsamea	*P. rubens*	
H_2O eluate:			
K	43.5 ± 6.71	69.0 ± 24.6	***
Ca	2.62 ± 1.62	2.87 ± 1.11	
Mg	10.0 ± 4.47	8.00 ± 4.47	***
Fe	2.26 ± 1.02	2.36 ± 1.34	
Mn	7.97 ± 3.33	7.93 ± 3.34	
Zn	6.25 ± 3.45	4.27 ± 2.21	
Cu	7.47 ± 2.92	8.06 ± 3.74	
EDTA extract:			
K	66.0 ± 8.94	89.0 ± 78.2	***
Ca	25.2 ± 11.8	19.9 ± 9.05	
Mg	63.5 ± 8.94	29.0 ± 4.47	**
Fe	45.2 ± 8.88	35.8 ± 6.88	*
Mn	100 ± 13.3	80.7 ± 10.7	**
Zn	94.2 ± 12.0	82.7 ± 8.26	*
Cu	29.7 ± 8.54	29.3 ± 9.18	**
$SrCl_2$ extract:			
K	76.5 ± 11.2	98.0 ± 82.7	***
Ca	38.5 ± 13.8	40.5 ± 16.9	
Mg	63.5 ± 8.94	48.0 ± 8.94	**
Fe	1.94 ± 0.93	2.99 ± 1.51	**
Mn	60.5 ± 9.63	69.1 ± 8.59	***
Zn	35.6 ± 8.78	44.6 ± 9.24	**
Cu	6.21 ± 2.56	9.03 ± 2.65	

Percentage value ± standard deviation related to the mean of total bark content in [mmol kg^{-1} DW] from the corresponding element. Statistics: U-test. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$; significances are between the two tree species. n = 20.

Tab. 4-A42. Confidence intervals of *Abies balsamea* of the different extraction media. n = 20.

	Arithmetic mean	Standard deviation	Lower limit	Upper limit
H_2O eluate:				
K	15.4	8.32	11.7	19.0
Mg	1.68	0.77	1.35	2.01
Ca	3.41	2.07	2.51	4.31
Zn	0.08	0.05	0.06	0.10
Cu	0.02	0.01	0.02	0.02
Mn	2.10	2.00	1.22	2.98
Fe	0.02	0.01	0.02	0.02
EDTA extract:				
K	23.2	12.1	17.9	28.4
Mg	5.36	2.17	4.40	6.32
Ca	35.5	22.9	25.5	45.5
Zn	1.21	0.43	1.01	1.41
Cu	0.07	0.02	0.07	0.07
Mn	22.7	14.1	16.6	28.9
Fe	0.53	0.23	0.43	0.63
$SrCl_2$ extract:				
K	25.9	12.5	20.5	31.4
Mg	10.7	5.90	8.14	13.3
Ca	51.5	24.6	40.7	62.3
Zn	0.43	0.11	0.37	0.49
Cu	0.02	0.01	0.02	0.02
Mn	13.7	9.40	9.57	17.8
Fe	0.02	0.01	0.02	0.02
Total content:				
K	36.5	25.0	27.4	45.7
Mg	16.7	9.12	13.3	20.1
Ca	133	47.2	113	154
Zn	1.26	0.32	1.12	1.40
Cu	0.26	0.08	0.22	0.30
Mn	22.7	14.4	16.4	29.0
Fe	1.20	0.45	1.00	1.40

Tab. 4-A43. Confidence intervals of *Picea rubens* of the different extraction media. n = 20.

	Arithmetic mean	Standard deviation	Lower limit	Upper limit
H_2O eluate:				
K	5.42	5.99	2.79	8.05
Mg	0.71	0.42	0.53	0.89
Ca	3.87	1.91	3.03	4.71
Zn	0.04	0.03	0.02	0.06
Cu	0.01	0.00	0.01	0.01
Mn	0.46	0.23	0.36	0.56
Fe	0.02	0.01	0.02	0.02
EDTA extract:				
K	8.49	9.59	4.30	12.7
Mg	2.55	1.45	1.92	3.18
Ca	25.7	11.9	20.5	30.9
Zn	1.14	1.40	0.53	1.75
Cu	0.05	0.02	0.05	0.05
Mn	5.04	2.25	4.06	6.02
Fe	0.45	0.28	0.33	0.57
$SrCl_2$ extract:				
K	10.1	12.0	4.81	15.3
Mg	4.27	2.55	3.15	5.39
Ca	50.3	15.1	43.7	56.9
Zn	0.59	0.76	0.26	0.92
Cu	0.02	0.00	0.02	0.02
Mn	4.24	1.70	3.50	4.98
Fe	0.03	0.01	0.03	0.03
Total content:				
K	15.2	18.4	8.02	22.3
Mg	8.38	3.46	7.14	9.65
Ca	144	69.0	144	175
Zn	1.34	1.56	0.65	2.03
Cu	0.19	0.06	0.17	0.21
Mn	6.20	2.62	5.06	7.34
Fe	1.25	0.74	0.92	1.58

Tab. 4-A44. Bivariate analysis of variance for the influence of the variables 'tree species' (B, R), 'cell type', and 'tree species and cell type' on the element content of bark.

	Total		Tree species (df=1)		Cell type (df=1)		Tree species × Cell type (df=1)	
	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value	Var. [%]	F value
Na	29	2.6 ***	0	0.2	19	2.6 ***	10	2.9 **
Mg	56	8.3 ***	4	15.7 ***	42	9.5 ***	10	4.9 ***
Al	43	4.7 ***	2	7.4 **	35	5.9 ***	6	2.1 *
Si	47	5.7 ***	16	56.2 ***	20	3.7 ***	11	4.2 ***
P	61	10.1 ***	14	65.2 ***	40	9.9 ***	8	4.2 ***
S	63	11.0 ***	0	0.2	45	11.9 ***	19	10.4 ***
Cl	46	5.5 ***	8	29.1 ***	21	3.7 ***	17	6.5 ***
K	84	34.2 ***	22	258.2 ***	53	32.6 ***	10	12.8 ***
Ca	69	14.4 ***	4	22.0 ***	49	15.7 ***	16	10.9 ***
Mn	82	28.9 ***	26	262.7 ***	46	24.7 ***	10	11.8 ***

Tab. 4-A45. Range (including minimum and maximum) and median of water-holding capacity of living (R) and dead (DR) *Picea rubens* as well as on living (B) and dead (DB) *Abies balsamea*. n =15.

	Min.	Max.	**Range**	Median
R	47.12	108.48	**61.36**	70.28
DR	46.65	80.04	**33.39**	61.90
B	26.52	130.46	**103.94**	69.16
DB	28.22	108.40	**80.18**	65.06

Tab. 4-A46. Spearman correlation matrix for the parameters measured in the bark of living *Picea rubens*.

	N	C	K	Ca	Mg	Fe	Mn	Zn	Pb	Cu	pH (H_2O)	pH (KCl)
C	.											
K	0.53**	.										
Ca	.	-0.46*	.									
Mg	.	.	.	.								
Fe	0.52**	.	.	.	.							
Mn	.	-0.50**	.	0.52**	0.53**	.						
Zn	.	-0.46*	.	0.44*	.	.	0.44*					
Pb	0.49**	.	.	.	.	0.43*	.	.				
Cu	0.76***	0.45*	.	.	.	.	.	.	0.44*			
pH (H_2O)	.	.	.	.	.	.	.	.	.	.		
pH (KCl)	.	.	.	.	.	.	.	.	.	.	0.85***	
Cond.	.	.	0.46*	.	.	.	.	.	.	.	-0.75***	-0.65***
	N	C	K	Ca	Mg	Fe	Mn	Zn	Pb	Cu	pH (H_2O)	pH (KCl)

Correlation coefficients are calculated from mean values of the 27 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A47. Spearman correlation matrix for the parameters measured in the bark of dead *Picea rubens*.

	N	C	K	Ca	Mg	Fe	Mn	Zn	Pb	Cu	pH (H_2O)	pH (KCl)
C	.											
K	.	.										
Ca	.	-0.41*	.									
Mg	.	.	0.38*	.								
Fe	.	.	.	-0.51**	.							
Mn	.	.	.	0.44*	0.56**	.						
Zn	0.41*	0.49**	.	0.64***	.	.	.					
Pb	.	.	.	-0.42*	.	.	.	.				
Cu	.	.	.	.	.	.	.	.	.			
pH (H_2O)	.	.	0.47*	.	0.47*	.	.	.	.	.		
pH (KCl)	.	.	0.43*	.	0.56**	.	0.46*	.	.	.	0.92***	
Cond.	.	.	.	0.56**	.	.	.	0.40*	.	0.47*	-0.48*	.
	N	C	K	Ca	Mg	Fe	Mn	Zn	Pb	Cu	pH (H_2O)	pH (KCl)

Correlation coefficients are calculated from mean values of the 27 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A48. Spearman correlation matrix for the parameters measured in the bark of living *Abies balsamea*.

	N	C	K	Ca	Mg	Fe	Mn	Zn	Pb	Cu	pH (H_2O)	pH (KCl)
C	.											
K	.	0.41*										
Ca	.	-0.60***	.									
Mg	.	.	0.65***	.								
Fe	.	.	-0.42*	-0.51**	-0.59**							
Mn	.	.	.	0.45*	.	.						
Zn	.	.	.	0.54**	.	.	0.75***					
Pb	.	.	.	.	.	.	.	.				
Cu	.	.	.	.	.	.	.	.	.			
pH (H_2O)	.	.	0.81***	0.39*	0.60***	-0.53**	.	.	.	.		
pH (KCl)	.	.	0.75***	0.43*	0.60***	-0.63***	0.51**	0.39*	.	0.39*	0.88***	
Cond.	.	.	0.76***	.	0.43*	.	.	.	.	.	0.47*	0.54**
	N	C	K	Ca	Mg	Fe	Mn	Zn	Pb	Cu	pH (H_2O)	pH (KCl)

Correlation coefficients are calculated from mean values of the 27 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A49. Spearman correlation matrix for the parameters measured in the bark of dead *Abies balsamea*.

	N	C	K	Ca	Mg	Fe	Mn	Zn	Pb	Cu	pH (H_2O)	pH (KCl)
C	.											
K	-0.53**	.										
Ca	.	-0.39*	.									
Mg	.	.	0.58**	0.64***								
Fe	.	.	.	.	.							
Mn	.	.	0.42*	0.51**	0.40*	.						
Zn	.	.	.	0.66***	0.65***	.	0.70***					
Pb	.	.	.	.	.	.	.	.				
Cu	.	.	.	.	.	.	.	.	.			
pH (H_2O)	.	.	0.50**	0.61***	0.67***	.	0.63***	0.61***	.	.		
pH (KCl)	.	.	0.47*	0.63***	0.69***	.	0.53**	0.60***	.	.	0.92***	
Cond.	.	.	0.59**	.	0.54**	.	0.39*	0.44*	.	.	.	.
	N	C	K	Ca	Mg	Fe	Mn	Zn	Pb	Cu	pH (H_2O)	pH (KCl)

Correlation coefficients are calculated from mean values of the 27 sample trees. Levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A50. Daily mean light intensity [%] of living (R) and dead (DR) *Picea rubens* as well as living (B) and dead (DB) *Abies balsamea* over a monthly period.

Date	R		DR		B		DB	
07.08.00	3.40 ± 2.70	a	6.90 ± 6.30	a	5.60 ± 4.90	a	4.50 ± 2.00	a
12.08.00	7.80 ± 2.20	a	9.30 ± 6.80	a	8.90 ± 7.50	a	7.10 ± 2.60	a
16.08.00	22.1 ± 19.3	a	22.8 ± 18.4	a	18.5 ± 15.0	a	20.8 ± 13.1	a
17.08.00	12.4 ± 7.80	a	13.1 ± 7.50	a	13.0 ± 6.50	a	14.2 ± 4.10	a
19.08.00	8.00 ± 3.30	a	9.20 ± 5.50	a	9.40 ± 5.20	a	10.4 ± 4.80	a
24.08.00	30.0 ± 12.5	a	30.3 ± 14.5	a	26.3 ± 16.3	a	23.6 ± 9.30	a
26.08.00	37.0 ± 16.5	a	28.6 ± 8.50	a	28.1 ± 10.7	a	36.2 ± 15.9	a
27.08.00	40.1 ± 12.9	a	40.8 ± 17.7	a	50.5 ± 18.8	a	52.9 ± 19.7	a
03.09.00[a]	19.2 ± 6.70	a	23.1 ± 12.7	a	21.4 ± 12.7	a	21.4 ± 5.50	a
03.09.00[b]	18.3 ± 9.10	a	24.0 ± 10.5	a	21.7 ± 10.8	ab	19.7 ± 5.90	ab
14.09.00[a]	6.80 ± 4.50	b	9.20 ± 6.40	ab	8.80 ± 5.80	ab	9.20 ± 3.80	a
14.09.00[b]	6.90 ± 4.50	b	9.90 ± 5.60	a	9.40 ± 5.60	a	8.50 ± 3.30	a
15.09.00[a]	19.6 ± 5.70	a	15.2 ± 5.20	b	16.4 ± 7.10	ab	17.2 ± 9.30	ab
15.09.00[b]	17.0 ± 5.90	a	16.0 ± 9.30	a	15.9 ± 6.80	a	17.4 ± 8.20	a
17.09.00	8.00 ± 3.20	a	9.10 ± 5.30	a	8.30 ± 4.20	a	9.40 ± 3.70	a

Arithmetic mean ± standard deviation. Statistics: U-test; $p \leq 0.05$. When not marked different or with [a]: n = 60, [b]: n = 99.

Tab. 4-A51. Daily evaporation [ml dm^{-2} d^{-1}] of living (R) and dead (DR) *Picea rubens* as well as living (B) and dead (DB) *Abies balsamea* over a monthly period.

Date	R	DR	B	DB
04.08.00	10.2 ± 3.30 a	9.60 ± 4.30 a	8.80 ± 2.70 a	9.60 ± 3.60 a
05.08.00	21.1 ± 4.80 a	18.5 ± 6.10 a	19.0 ± 4.90 a	18.5 ± 6.40 a
06.08.00	28.4 ± 4.30 a	35.9 ± 35.4 ab	26.3 ± 4.20 a	22.1 ± 4.50 b
07.08.00	2.40 ± 2.20 a	3.50 ± 5.50 a	2.83 ± 0.94 a	2.40 ± 0.68 a
08.08.00	3.50 ± 2.90 a	5.40 ± 4.00 a	5.80 ± 3.70 a	4.40 ± 3.30 a
09.08.00	6.90 ± 4.50 a	5.50 ± 3.70 a	8.20 ± 4.40 a	6.10 ± 3.80 a
10.08.00	9.30 ± 2.90 a	10.6 ± 4.40 a	10.9 ± 4.10 a	9.30 ± 4.10 a
11.08.00	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a
12.08.00	5.40 ± 2.60 ab	6.20 ± 2.00 b	5.10 ± 1.50 ab	4.40 ± 1.40 a
13.08.00	10.0 ± 3.00 a	11.3 ± 4.10 a	10.9 ± 3.20 a	9.40 ± 4.90 a
14.08.00	9.90 ± 0.94 a	9.10 ± 2.20 a	11.2 ± 3.40 a	8.10 ± 1.50 a
15.08.00	6.40 ± 2.20 a	6.10 ± 2.50 a	7.50 ± 2.30 a	5.40 ± 3.30 a
16.08.00	8.60 ± 10.0 a	4.40 ± 1.90 a	4.70 ± 1.90 a	3.70 ± 1.80 a
17.08.00	0.14 ± 0.45 a	0.14 ± 0.45 a	0.00 ± 0.00 a	0.14 ± 0.45 a
18.08.00	4.80 ± 2.80 a	5.80 ± 3.40 a	5.90 ± 2.80 a	4.50 ± 3.30 a
19.08.00	9.30 ± 2.30 b	6.80 ± 2.80 a	6.50 ± 2.60 a	9.10 ± 4.30 ab
20.08.00	5.10 ± 2.10 a	5.90 ± 2.30 a	6.80 ± 3.40 a	5.50 ± 1.40 a
21.08.00	12.9 ± 3.00 a	11.6 ± 3.80 a	11.0 ± 4.10 a	10.6 ± 3.90 a
22.08.00	21.9 ± 4.70 a	23.8 ± 6.20 a	22.9 ± 4.00 a	19.7 ± 5.00 a
23.08.00	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a	0.00 ± 0.00 a
24.08.00	11.6 ± 3.40 a	9.20 ± 2.10 ab	8.50 ± 2.90 a	7.60 ± 1.40 a
25.08.00	9.30 ± 6.30 a	10.6 ± 5.70 a	9.60 ± 4.10 a	7.90 ± 5.00 a
26.08.00	21.2 ± 5.10 ab	22.1 ± 4.90 b	21.1 ± 4.60 ab	17.8 ± 3.60 a
27.08.00	4.40 ± 2.60 a	3.50 ± 1.20 a	4.50 ± 1.70 a	3.10 ± 1.60 a
28.08.00	26.6 ± 5.50 a	28.6 ± 5.30 a	27.2 ± 6.80 a	21.8 ± 2.80 b
29.08.00	25.6 ± 3.40 a	25.3 ± 4.50 a	23.9 ± 4.10 a	20.4 ± 3.20 b
30.08.00	16.0 ± 3.20 a	17.1 ± 4.50 a	16.7 ± 3.80 a	13.6 ± 4.50 a
31.08.00	14.7 ± 5.10 a	15.6 ± 4.80 a	13.6 ± 3.70 a	12.6 ± 3.20 a
01.09.00	13.2 ± 2.80 a	13.3 ± 3.50 a	13.4 ± 2.80 a	11.2 ± 4.10 a
02.09.00	1.40 ± 0.67 a	0.71 ± 0.75 b	0.85 ± 0.99 ab	0.71 ± 1.00 ab
03.09.00	0.00 ± 0.00 a	0.00 ± 0.00 a	0.14 ± 0.45 a	0.28 ± 0.89 a

Arithmetic mean ± standard deviation. Statistics: U-test; $p \leq 0.05$. n = 40.

Tab. 4-A52. Linear multiple correlation analysis for lichen cover of which correlates with more than one element concentration in stem flow.

	n	R	F, p	
Flavopunctelia soredica	1	0.28	3.20	NO_3^-
	2	0.28	1.58	NO_3^-, Ca
Hypogymnia physodes	1	0.43	8.30 **	NO_3^-
	2	0.48	5.30 **	NO_3^-, Ca
Usnea spec.	1	0.39	6.81 *	NO_3^-
	2	0.46	4.96 *	NO_3^-, Ca
Platismatia glauca	1	0.34	5.06 *	NO_3^-
	2	0.42	3.90 *	NO_3^-, Mn
Mycoblastus sanguinarius	1	0.38	6.34 *	Mn
	2	0.45	4.49 *	Mn, NO_3^-
	3	0.45	2.94 *	Mn, NO_3^-, Ca
Parmelia saxatilis	1	0.62	22.6 ***	Mn
	2	0.65	13.2 ***	Mn, Mg
	3	0.67	9.25 ***	Mn, Mg, NO_3^-
	4	0.67	6.77 ***	Mn, Mg, NO_3^-, Ca
	5	0.67	5.25 ***	Mn, Mg, NO_3^-, Ca, S
Micarea prasina	1	0.32	4.15 *	S
	2	0.39	3.14	Mn, Ca
	3	0.39	2.10	Mn, Ca, S
Cladonia coniocraea	1	0.40	7.34 *	S
	2	0.41	3.79 *	S, Fe

Linear regression with logarithmized data (independent variables: x = ln x‘; dependent variables: y = [y‘ + 1]). Data from *Cladonia coniocraea* from 1999, otherwise 2000.
n: number of dependent variables in the model. R: multiple correlation coefficient. F, p: F values and levels of significance: * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Tab. 4-A53. Correlation coefficient and significance of selected lichen species related to element content [mmol kg^{-1} DW] of extraction with H_2O. Regression model: a/(b*x). n = 40.

	K		Ca		Mg		Mn		Zn		Fe		Cu	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p
Cladonia coniocraea	-0.39	*	.		-0.34	*	-0.42	**	-0.37	*	.		.	
Flavopunctelia soredica	.		-0.34	*	.		.		.		.		.	
Imshaugia aleurites	-0.45	**	.		-0.33	*	-0.32	*	.		.		.	
Lecidea nylanderi	-0.46	**	.		-0.36	*	-0.37	*	-0.37	*	.		.	
Lepraria jackii	-0.39	*	-0.35	*	-0.35	*	-0.44	**	-0.41	**	.		.	
Mycoblastus sanguinarius	.		.		.		.		.		.		.	
Platismatia glauca	.		.		.		.		.		.		.	
Pseudevernia cladonia	-0.33	*	-0.42	**	.		.		.		.		.	
Usnea spec.	.		.		.		.		.		.		.	

Tab. 4-A54. Correlation coefficient and significance of selected lichen species related to element content [mmol kg^{-1} DW] of extraction with EDTA. Regression model: a/(b*x). n = 40.

	K		Ca		Mg		Mn		Zn		Fe		Cu	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p
Cladonia coniocraea	-0.40	*	.		-0.35	*	-0.43	**	-0.32	*	.		.	
Flavopunctelia soredica	.		-0.36	*	.		.		.		.		.	
Imshaugia aleurites	-0.44	**	-0.31	*	-0.33	*	-0.32	*	.		.		.	
Lecidea nylanderi	.		.		-0.36	*	-0.33	*	.		.		.	
Lepraria jackii	-0.40	*	.		.		-0.42	**	-0.38	*	.		.	
Mycoblastus sanguinarius	.		.		.		.		.		.		.	
Platismatia glauca	.		.		.		.		.		.		.	
Pseudevernia cladonia	.		-0.46	**	-0.37	*	.		.		-0.41	**	.	
Usnea spec.	.		.		.		.		.		-0.34	*	.	

Tab. 4-A55. Correlation coefficient and significance of selected lichen species related to element content [mmol kg^{-1} DW] of extraction with $SrCl_2$. Regression model: a/(b*x). n = 40.

	K		Ca		Mg		Mn		Zn		Fe		Cu	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p
Cladonia coniocraea	-0.39	*	.		-0.37	*	-0.40	*	.		.		.	
Flavopunctelia soredica	.		-0.31	*	.		.		.		.		.	
Imshaugia aleurites	-0.44	**	.		-0.34	*	.		.		.		.	
Lecidea nylanderi	.		.		-0.36	*	-0.33	*	.		.		.	
Lepraria jackii	-0.40	*	.		-0.38	*	-0.41	**	.		.		.	
Mycoblastus sanguinarius	.		.		.		.		.		.		.	
Platismatia glauca	.		.		.		.		.		.		.	
Pseudevernia cladonia	-0.35	*	-0.39	*	-0.38	*	.		.		.		.	
Usnea spec.	.		.		.		.		.		.		.	

Tab. 4-A56. Correlation coefficient and significance of selected lichen species related to total bark content [mmol kg^{-1} DW] extracted with HNO_3. Regression model: a/(b*x). n = 40.

	K		Ca		Mg		Mn		Zn		Fe		Cu	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p
Cladonia coniocraea	.		.		.		-0.41	**	.		.		.	
Flavopunctelia soredica	.		.		.		.		.		.		.	
Imshaugia aleurites	.		.		.		.		.		.		.	
Lecidea nylanderi	.		.		.		-0.33	*	.		.		.	
Lepraria jackii	.		.		.		-0.41	**	.		.		.	
Mycoblastus sanguinarius	.		.		.		.		.		.		.	
Platismatia glauca	.		.		.		.		.		.		.	
Pseudevernia cladonia	.		.		.		.		.		-0.34	*	.	
Usnea spec.	.		-0.33	*	.		.		.		.		.	

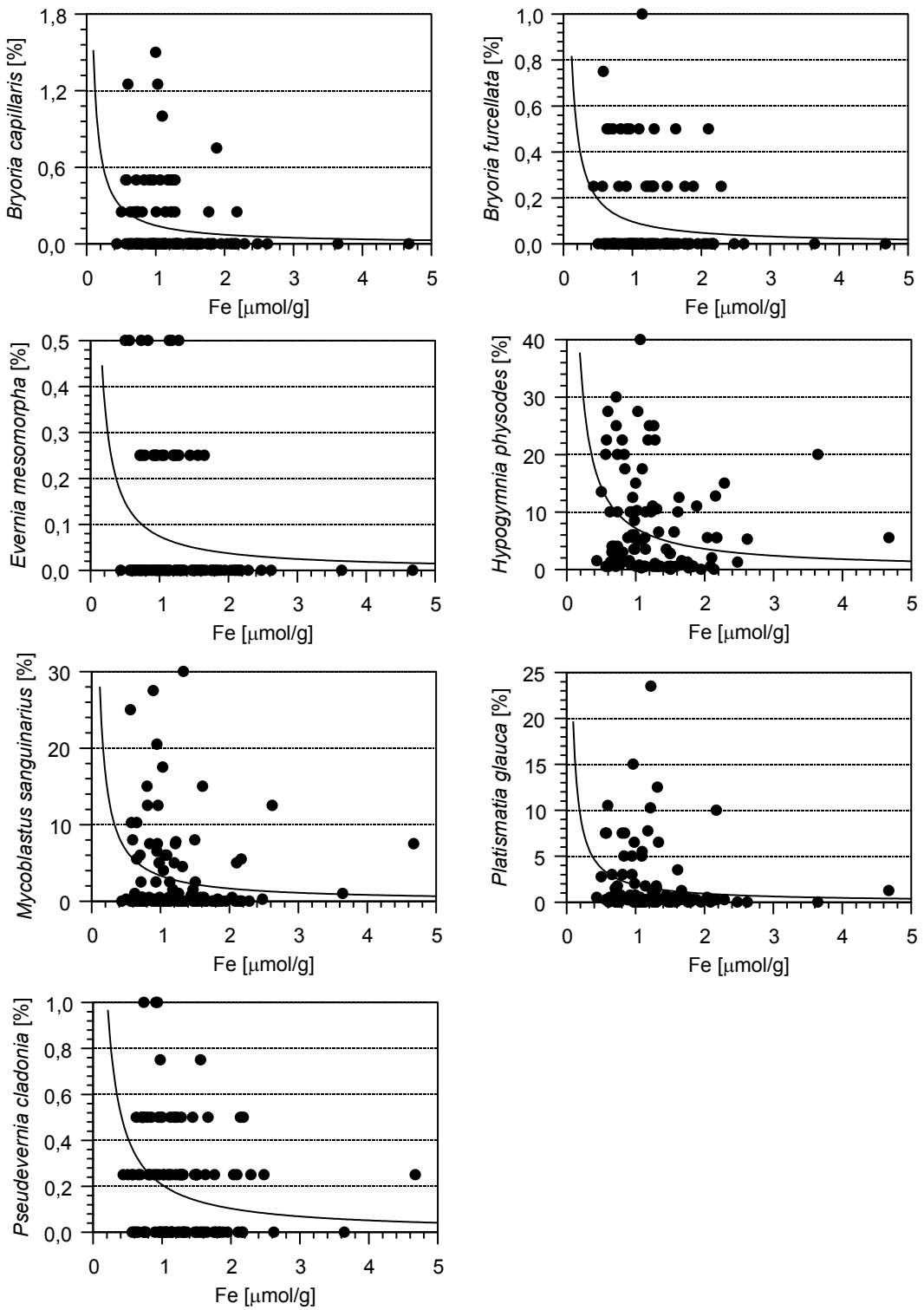

Fig. 4-A1. Correlation between lichen species and Fe content in the bark. Regression model: a/(b*x). n = 40. *B. capillaris*: r = -0.20, $p \leq 0.05$; *B. furcellata*: r = -0.20, $p \leq 0.05$; *E. mesomorpha*: r = -0.20, $p \leq 0.05$; *H. physodes*: r = -0.33, $p \leq 0.001$; *M. sanguinarius*: r = -0.22, $p \leq 0.05$; *P. glauca*: r = -0.20, $p \leq 0.05$; *P. cladonia*: r = -0.33, $p \leq 0.001$.

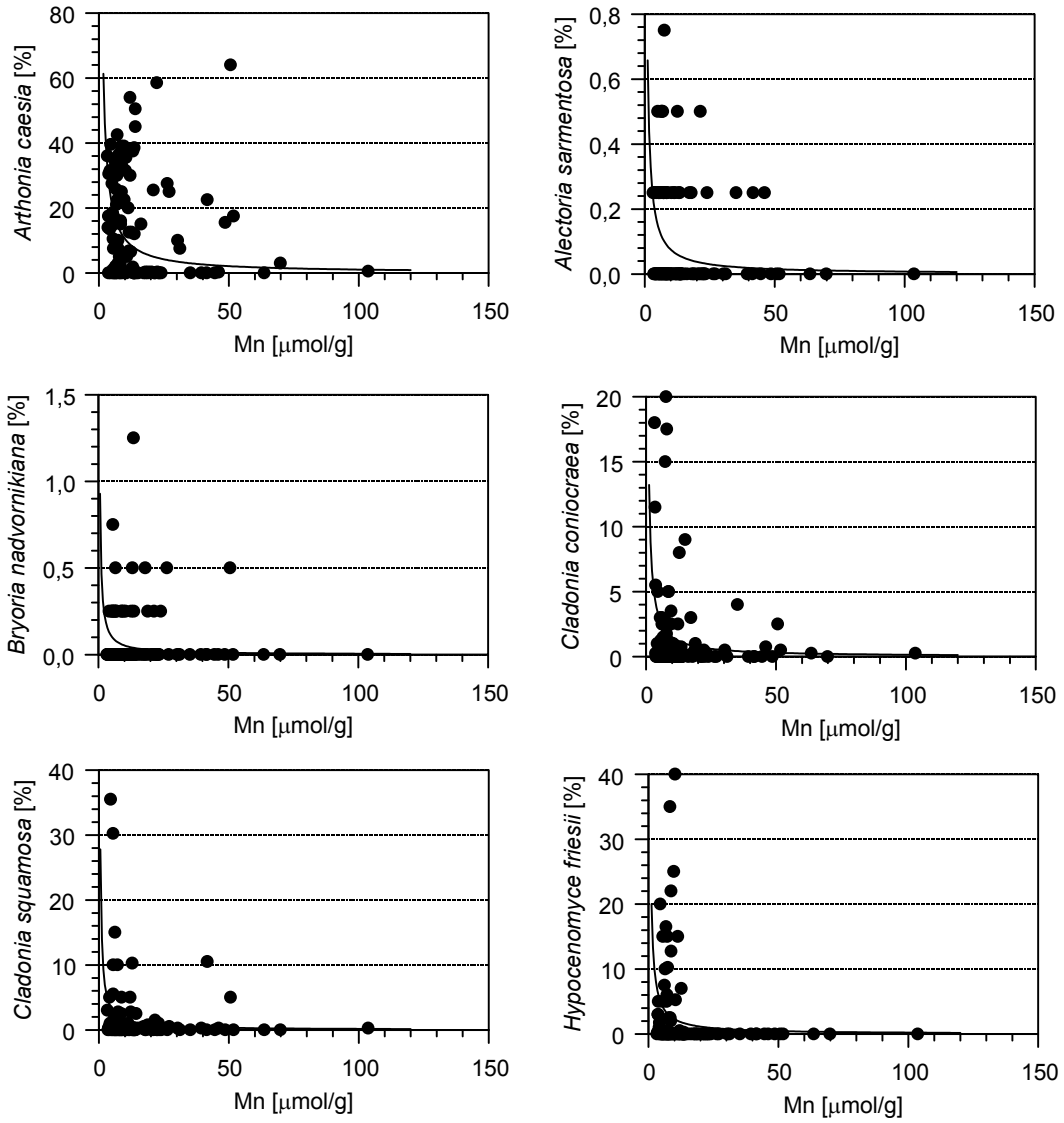

Fig. 4-A2. Correlation between lichen species and Mn content in the bark. Regression model: a/(b*x). n = 40. *A. caesia*: r = -0.44, $p \leq 0.001$; *A. sarmentosa*: r = -0.32, $p \leq 0.001$; *B. nadvornikiana*: r = -0.19, $p \leq 0.05$; *C. coniocraea*: r = -0.27, $p \leq 0.01$; *C. squamosa*: r = -0.21, $p \leq 0.05$; *H. friesii*: r = -0.22, $p \leq 0.05$.

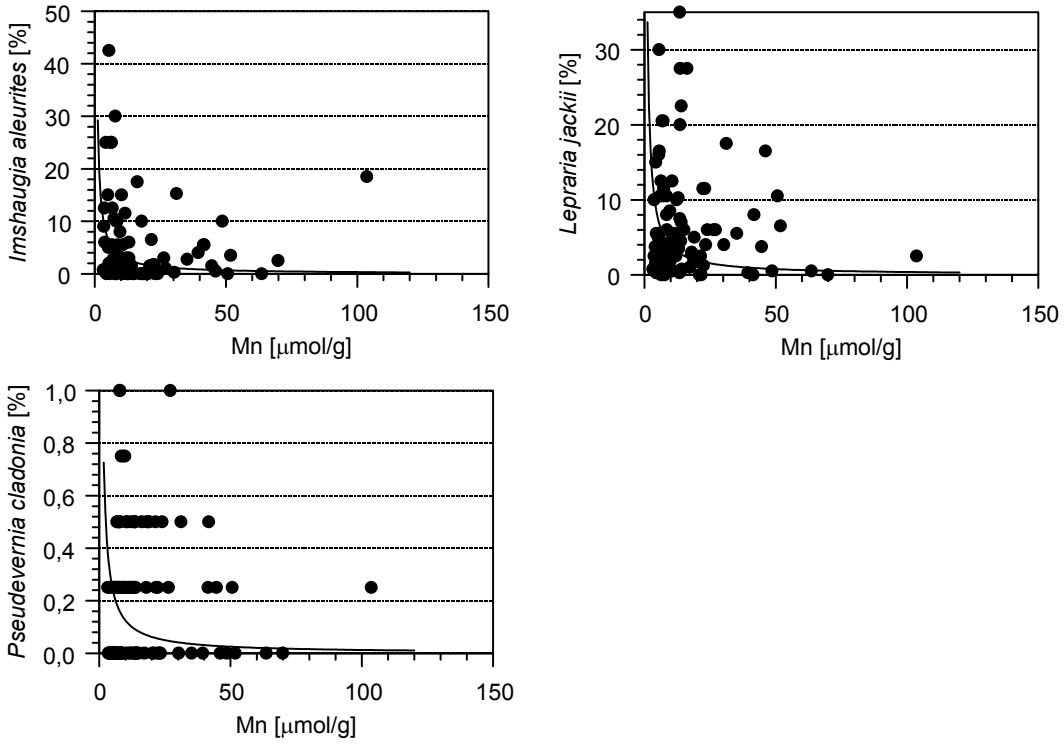

Fig. 4-A3. Correlation between lichen species and Mn content in the bark. Regression model: a/(b*x). n = 40. *I. aleurites*: r = -0.31, $p \leq 0.01$; *L. jackii*: r = -0.36, $p \leq 0.001$; *P. cladonia*: r = -0.34, $p \leq 0.001$.

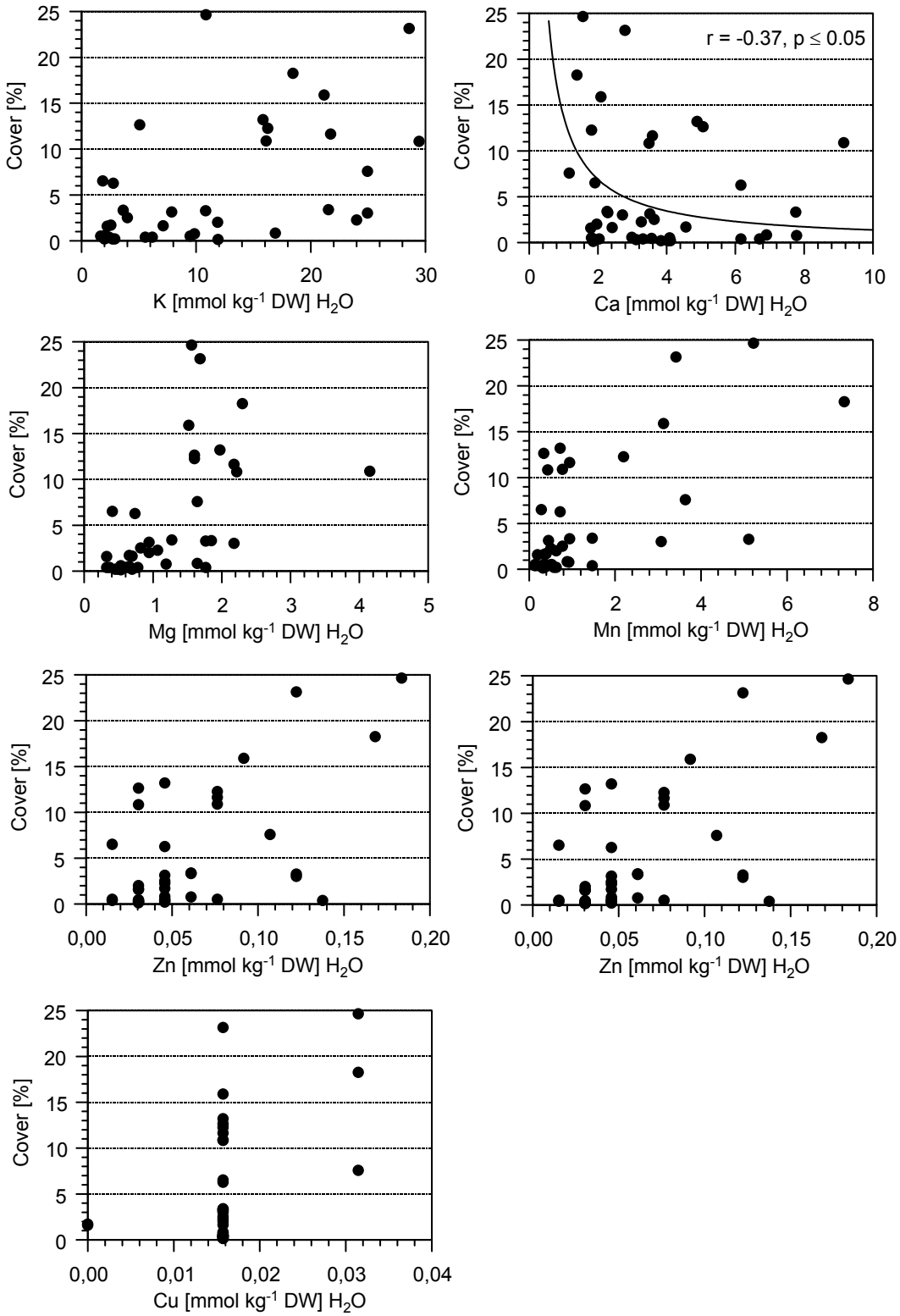

Fig. 4-A4. Lichen cover of *Hypogymnia physodes* vs. element content of extraction with H_2O. Regression model: a/(b*x). n = 40.

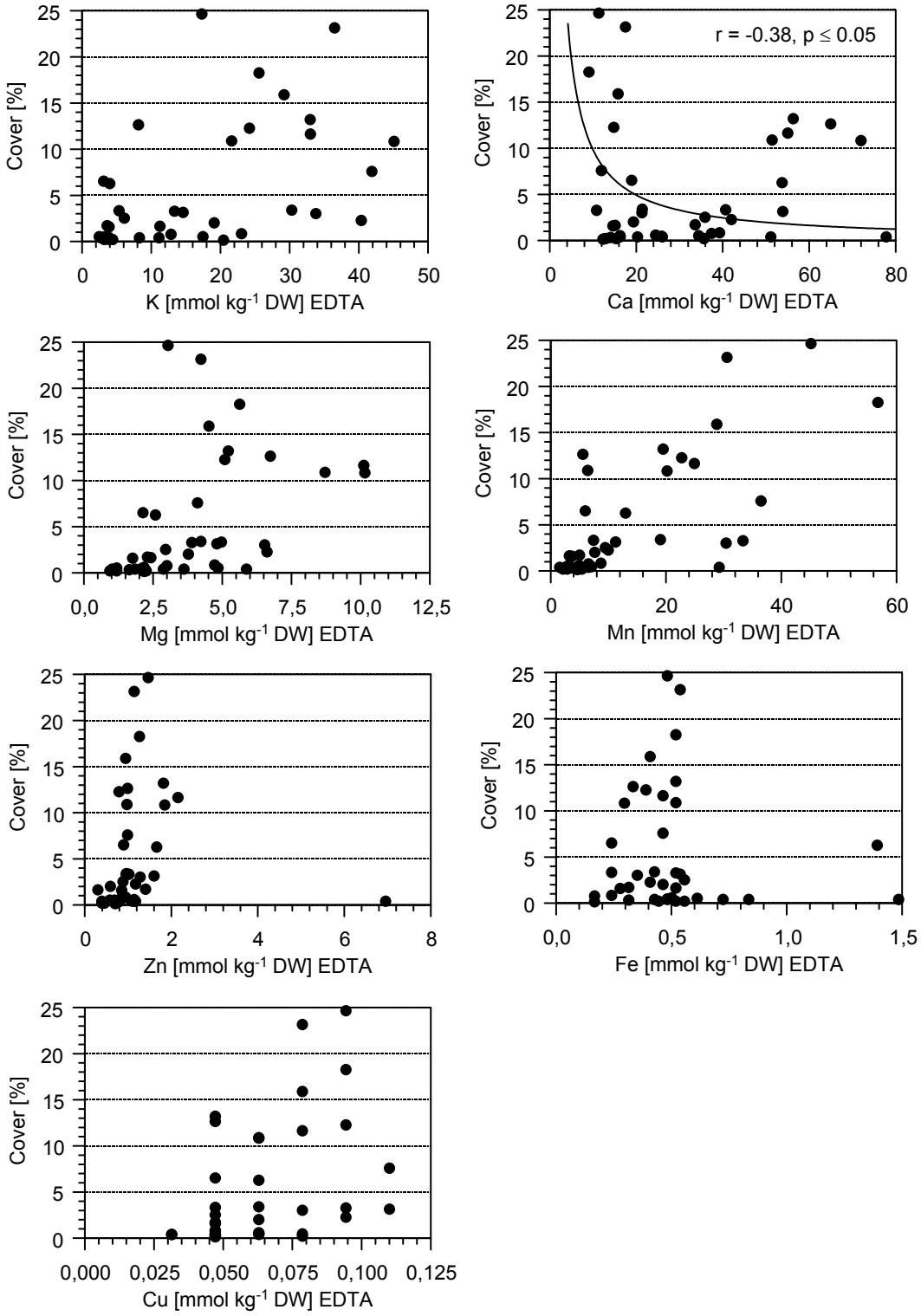

Fig. 4-A5. Lichen cover of *Hypogymnia physodes* vs. element content of extraction with EDTA. Regression model: a/(b*x). n = 40.

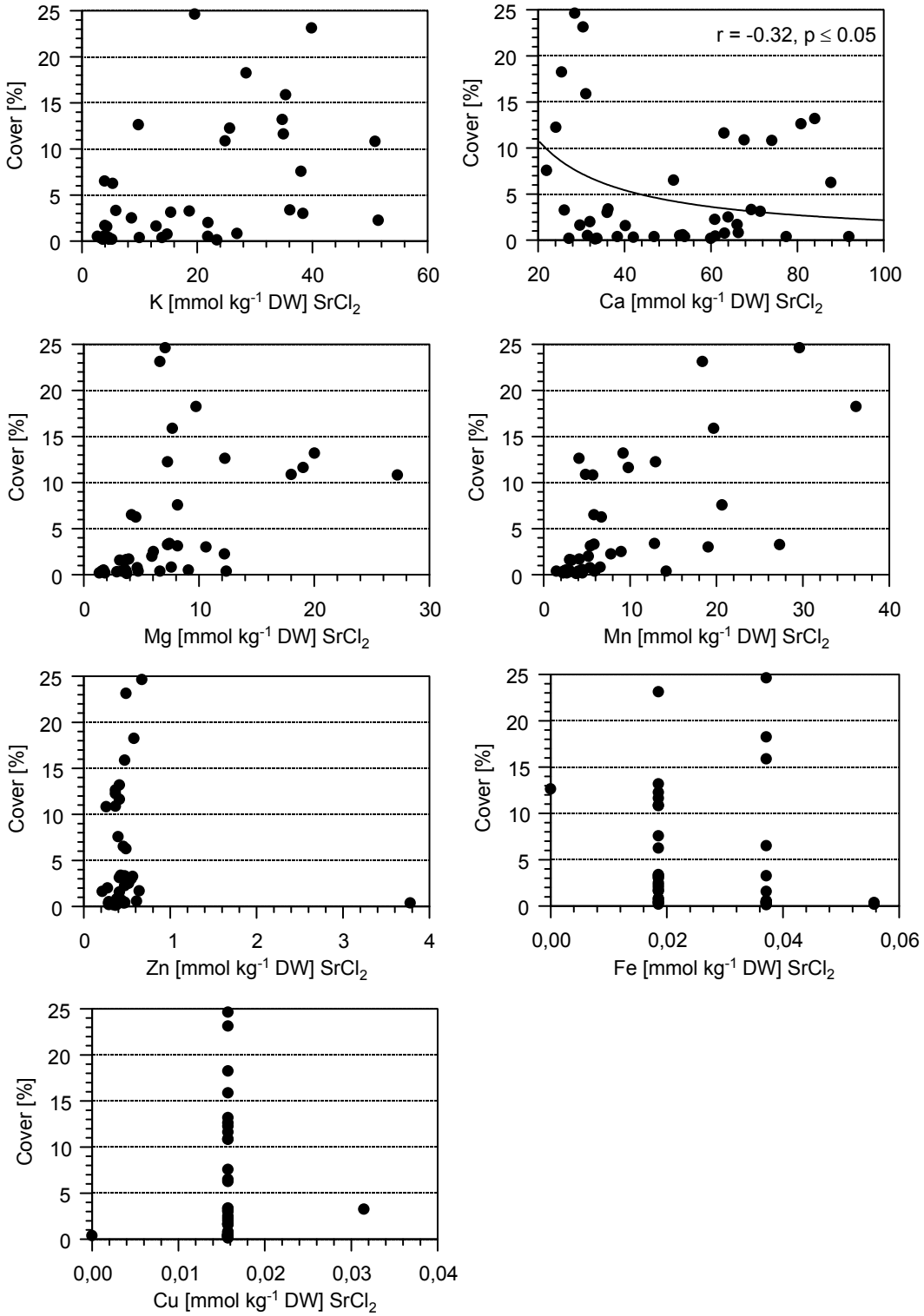

Fig. 4-A6. Lichen cover of *Hypogymnia physodes* vs. element content of extraction with $SrCl_2$. Regression model: a/(b*x). n = 40.

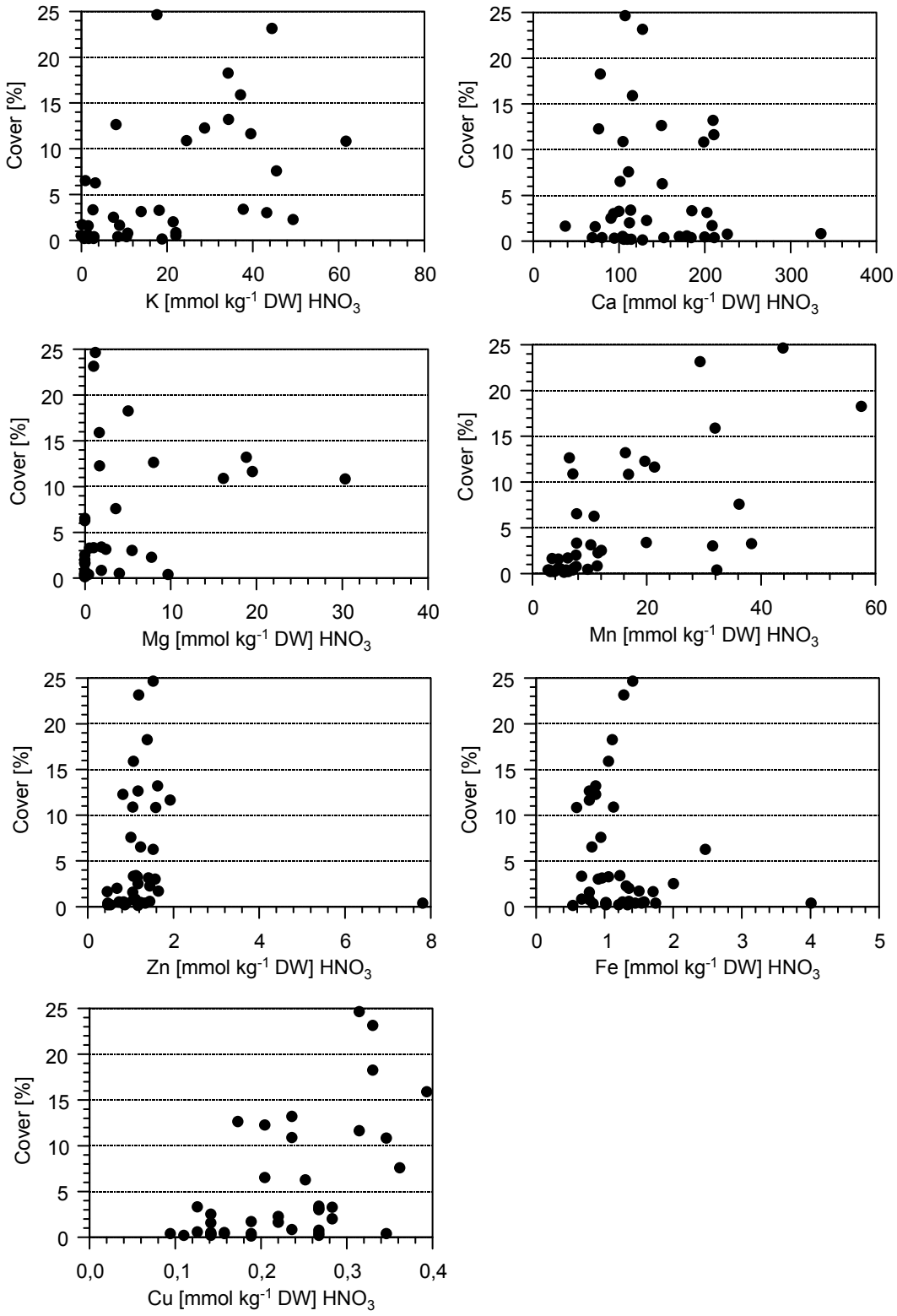

Fig. 4-A7. Lichen cover of *Hypogymnia physodes* vs. element content of extraction with HNO_3. Regression model: a/(b*x). n = 40.

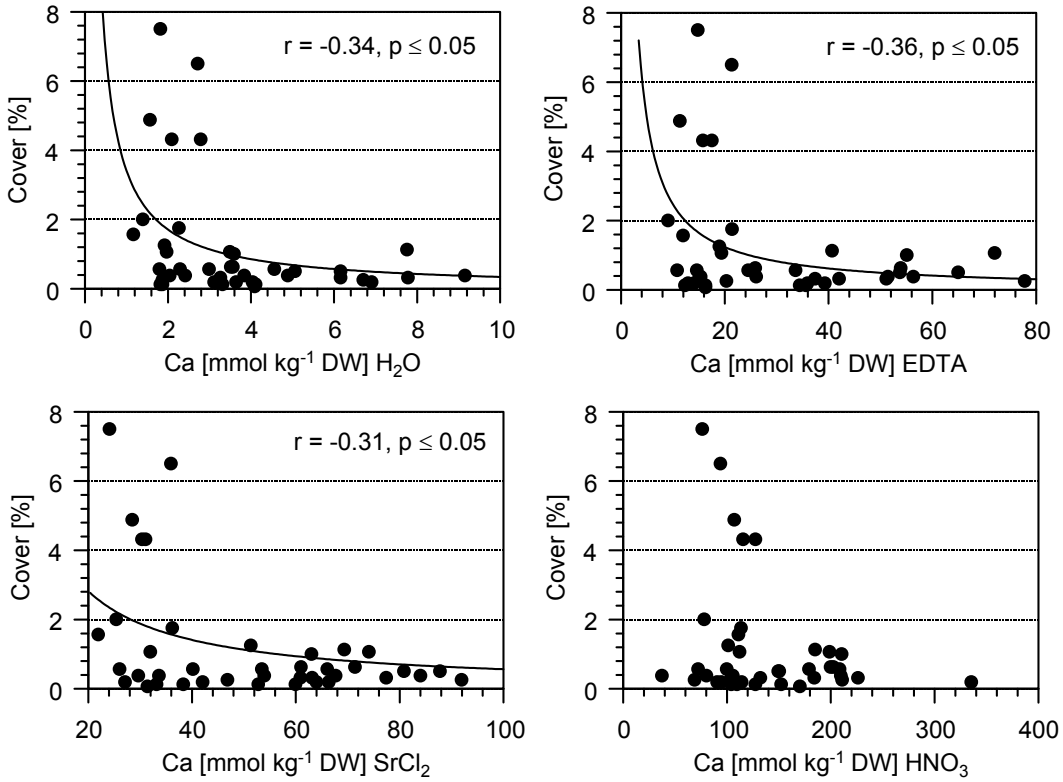

Fig. 4-A8. Lichen cover of *Flavopunctelia soredica* vs. element content of extraction with H_2O, EDTA, $SrCl_2$, and HNO_3. Regression model: a/(b*x). n = 40.

Curriculum vitae

November 17, 1971	Born in Kiel, Schleswig-Holstein, Germany.
1991	Graduation from Gymnasium (Secondary School) in Alfeld, Lower Saxony, Germany, with ‚Abitur' certificate.
1991-1992	Volunteer in ecology (Freiwilliges Ökologisches Jahr) in Lower Saxony (Energie- und Umweltzentrum, Eldagsen), Germany.
1992	Enrollment at the Biological Faculty of the Georg August University at Göttingen.
1995-1996	Studies at Trinity College Dublin, Ireland.
1998	Diploma as biologist at the University of Göttingen; examinations: botany, microiology, and soil science; thesis in botany on ecology of *Quercus robur*, *Q. petraea*, and *Fagus sylvatica*.
1999-2002	Doctorand at the Department of Ecology and Ecosystem Research of the Albrecht von Haller Institute of Plant Sciences at the University of Göttingen.