

## Eutrophication threatens the biochemical diversity in lichens

Markus HAUCK

**Abstract:** Lichens respond sensitively to ambient nitrogen levels. Global change, which includes the increase of nitrogen-polluted environments, causes the decline of species sensitive to eutrophication, whereas some species tolerant of high nitrogen levels increase. Lichens produce hundreds of carbon-based secondary substances (so-called lichen substances), most of which are unique to the lichen symbiosis. In the present paper, correlative patterns between the eutrophication tolerance of lichen species and their secondary chemistry are analyzed using two data sets, one classifying the eutrophication tolerance of more than 500 Central European lichen species, and another of epiphytic lichens from more than 1200 plots from the Netherlands. Analyses show that, in general, the diversity of lichen secondary metabolites decreases along with increasing tolerance to eutrophication. Most notable is the reduced diversity of depsides and depsidones, the two largest groups of lichen substances, but dibenzofurans and fatty acids are also generally found in lichens sensitive to eutrophication. Conversely, anthraquinones and pulvinic acids are found most frequently in lichens from nitrogen-rich environments that can result from eutrophication. A family-wide analysis of the datasets indicates that loss of chemical diversity is not due to a single species-rich lichen family, but a characteristic of many lichen families.

**Key words:** biodiversity, global change, lichen-forming fungi, lichen substances, nitrogen, secondary metabolites

---

### Introduction

In addition to global warming, the global increase in nitrogen pollution in the atmosphere and across a wide range of ecosystems is a major threat to biodiversity (Krupa 2003). Since most nitrogen emissions derive from the agricultural sector (Olivier *et al.* 1998; Webb *et al.* 2005) and the human population is over-exponentially increasing, a reduction of the nitrogen pools currently accumulating in most ecosystems all over the world is not in sight. Lichens are known to be sensitive to nitrogen pollution (Hauck 2010). While evidence on noxious effects of high concentrations of nitrate (Schmull *et al.* 2002) or nitric acid (Riddell *et al.* 2008) in precipitation are scarce, ammonia is well documented to damage cytoplasmic membranes and to reduce the chlorophyll fluo-

rescence yield at photosystem II (Munzi *et al.* 2009a, b; Pirintsos *et al.* 2009). Detailed surveys, especially of the epiphytic lichen vegetation in highly nitrogen-polluted areas, showed that many species decline at high nitrogen levels, whereas other eutrophication-tolerant or even nitrogen-demanding species increase (van Dobben & ter Braak 1998, 1999; van Herk 1999). With decreasing nitrogen levels, as regionally found in the Netherlands, these shifts in lichen vegetation can partly be reversed (Sparrius 2007), though many nitrogen-sensitive species with dispersal limitations do not survive temporary peaks of nitrogen pollution.

Since recent investigations have suggested that the production of lichen substances is involved in the uptake and tolerance of lichens to cations including various metals and protons (Hauck & Jürgens 2008; Hauck *et al.* 2009a, b), the present study investigated whether the ambient nitrogen level influences biochemical diversity of lichen vegetation. Specifically, the hypothesis was tested that the diversity of lichen secondary

---

M. Hauck: Department of Plant Ecology, Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany. Email: mhauck@gwdg.de

TABLE 1. Definition of indicator values estimating eutrophication tolerance of Central European lichens (Wirth 2010)

Class in Wirth (2010)	Definition	Class of eutrophication tolerance in the present study	<i>n</i> *
N1	Tolerating nearly no eutrophication	Low	83
N2	Between N1 and N3	Low	125
N3	Tolerating slight eutrophication	Low	82
N4	Between N3 and N5	Moderate	62
N5	Tolerating moderate eutrophication	Moderate	46
N6	Between N5 and N7	Moderate	44
N7	Tolerating strong eutrophication	High	34
N8	Between N7 and N9	High	28
N9	Tolerating very strong eutrophication	High	12

\**n*, number of lichen species included in the study (total number of species is 516)

metabolites is reduced at high nitrogen levels. To test this hypothesis, a macroecological approach was applied linking published data on the eutrophication tolerance of lichens from Europe with the known secondary chemistry of the species. Two different data sets were employed which rank European lichen species after their eutrophication tolerance. The first supra-regional data set provides indicator values across a range of more than 500 species of lichen-forming ascomycetes (Wirth 2010). The second data set derives from a regional study of the epiphytic lichen vegetation in the Netherlands, which was selected as a case example because of the extraordinarily high levels of ammonia pollution in this area (van Dobben & de Bakker 1996). Analyses were conducted on the species and for the first data set also at the family level. The family-wise analysis was included in order to test the hypothesis that the correlations between the diversity of lichen substances and the eutrophication tolerance are not merely due to the individual traits of a few species-rich families, including the *Parmeliaceae*, *Physciaceae* and *Teloschistaceae*.

## Materials and Methods

### Sources for vegetation and nitrogen-tolerance data

For the supra-regional analysis of Central European lichen species, indicator values were extracted from Wirth (2010). The methodology for obtaining these

values is based on the ecological indicator values introduced by Ellenberg (1974, 1992) for vascular plants. These indicator values have repeatedly been used for ecological analyses in vascular plants, but rarely in lichens (Hauck & Wirth 2010). Eutrophication tolerance is estimated with these indicator values on a nine-point scale (Table 1). Wirth (2010) includes a total of 516 species of lichens and closely related fungi, which is c. 15–20% of the Central European lichen flora. The 516 species include 510 lichen-forming ascomycetes, three closely related non-lichenized ascomycetes (belonging to the *Microcaliciaceae* and *Mycocaliciaceae*), and two lichen-forming basidiomycetes. For the data analyses in the present study, the nine-point scale of Wirth (2010) is converted into a three-point scale of eutrophication tolerance (low, moderate, high), also shown in Table 1.

A regional assessment of the eutrophication tolerance of specific epiphytic lichen species was extracted from van Dobben & de Bakker (1996). This study includes eight study areas representative of different regions of the Netherlands. In these areas, a total of 1216 sampling points (each with up to ten broad-leaved trees) was sampled. Based on these data and the known atmospheric ammonia mean concentrations of the individual areas, the species were classified as eutrophication-tolerant nitrophytes, eutrophication-sensitive acidophytes or indifferent towards the nitrogen supply in a canonical correspondence analysis. All species classified by van Dobben & de Bakker (1996) as eutrophication-tolerant (*n* = 18) and eutrophication-sensitive (*n* = 15) are included in the present analysis.

### Sources for data on lichen secondary chemistry and phylogenetic relationships

Secondary chemistry of relevant lichen species listed in van Dobben & de Bakker (1996) or all 516 species included in Wirth (2010) was extracted from the literature (e.g. Wirth 1995; Smith *et al.* 2009). Secondary metabolites were assigned to classes of lichen substances using Huneck & Yoshimura (1996) and Huneck (2001). In the case of lichen substances occurring in chemosyndromes, only the main compounds were included,

because closely related compounds of one chemosyn-drome reflect interstage- or by-products or even decay products, for which in many cases no known biological function is assumed, at least not if these compounds occur in low concentrations (Leuckert 1985; Søchting 1997). Species listed in Wirth (2010) were assigned to families based on Lumbsch & Huhndorf (2007) and modifications compiled in Smith *et al.* (2009).

#### Data analysis

Two target variables are analyzed: 1) the percentage of all lichen species with a given eutrophication tolerance producing the relevant compound or class of compounds; 2) the number of lichen substances produced by the lichen species of a given level of eutrophication tolerance. Analyses were limited to the quantitatively most important substance classes of the depsides, depsidones, dibenzofurans, xanthenes, fatty acids, triterpenoids, pulvinic acids (i.e. tetric acid derivatives), and anthraquinones. Statistical significance of differences in the frequencies of data sets is tested with the chi-square test. Yates' correction of chi-square values is applied in the regional data set, which is characterized by a limited set of lichen species and, with it, lichen substances.

## Results

### Secondary chemistry and eutrophication tolerance of more than 500 Central European lichens

Altogether 125 lichen substances are known to be produced by the species treated by Wirth (2010). Most of these substances are rare, with 88% occurring in less than 1% of the studied species. Only a few depsides (atranorin as well as gyrophoric, lecanoric, thamnolic and squamatic acids), depsidones (norstictic, fumarprotocetraric and stictic acids) and dibenzofurans (usnic acid) occur in more than 10% of the more than 500 analyzed lichen species (data not shown). Depsides and depsidones are the most frequent classes of lichen substances in the studied lichens (Fig. 1A). Both substance classes and the dibenzofurans are significantly more frequent in lichen species from nitrogen-poor sites than in species with high tolerance to eutrophication. By contrast, anthraquinones and pulvinic acids occur more frequently in lichens with high nitrogen tolerance than in eutrophication-sensitive species. However, the number of anthraquinones and pulvinic acids is much lower

than that of depsides and depsidones (Fig. 1B). The frequent occurrence of anthraquinones in eutrophication-tolerant lichens is due to the abundance of a single substance, parietin, which is produced by 20% of the highly tolerant species, but by only 9% of species with moderate tolerance and only 5% with low tolerance.

The total diversity of depsides, depsidones and fatty acids decreases along with eutrophication tolerance, whereas there is no such trend for xanthenes and pulvinic acids and only a weak tendency for anthraquinones and triterpenoids (Fig. 1B). The dibenzofurans show a trend for more substances occurring in lichens with low eutrophication tolerance than in other lichens, but this trend is not significant ( $P = 0.08$ ). Except for the xanthenes, almost all lichen substances studied occur in species of low eutrophication tolerance (Fig. 1B). A major impoverishment of lichen substances is already observed in species of moderate eutrophication tolerance (Fig. 1B). In the largest classes of lichen substances, namely depsides and depsidones, further impoverishment occurs between species of moderate and high eutrophication tolerance, but not as steep as between species of moderate and low tolerance (Fig. 1B). The proportion of lichen species which do not produce lichen substances increases with increasing tolerance to high nitrogen levels (Fig. 1A).

The 516 analyzed species represent 55 families of ascomycetes (509 species) and one family of basidiomycetes (2 species). Five lichen-forming ascomycetes could not be assigned to a family (*Cystocoleus*, *Leprocaulon*, *Petractis*, *Racodium*, *Strangospora*). Most families contain only a few relevant species. Only 13 families include at least 10 relevant species; overall 68% of the 516 species belong to these 13 families. Table 2 shows the number of lichen substances found in the species of these 13 families. In none of these 13 families are all lichen substances of a certain substance group produced, not even in the *Parmeliaceae*, which harbour the highest diversity of lichen substances and species (Table 2) among the lichen families studied. Even in the *Parmeliaceae*, 20 out of

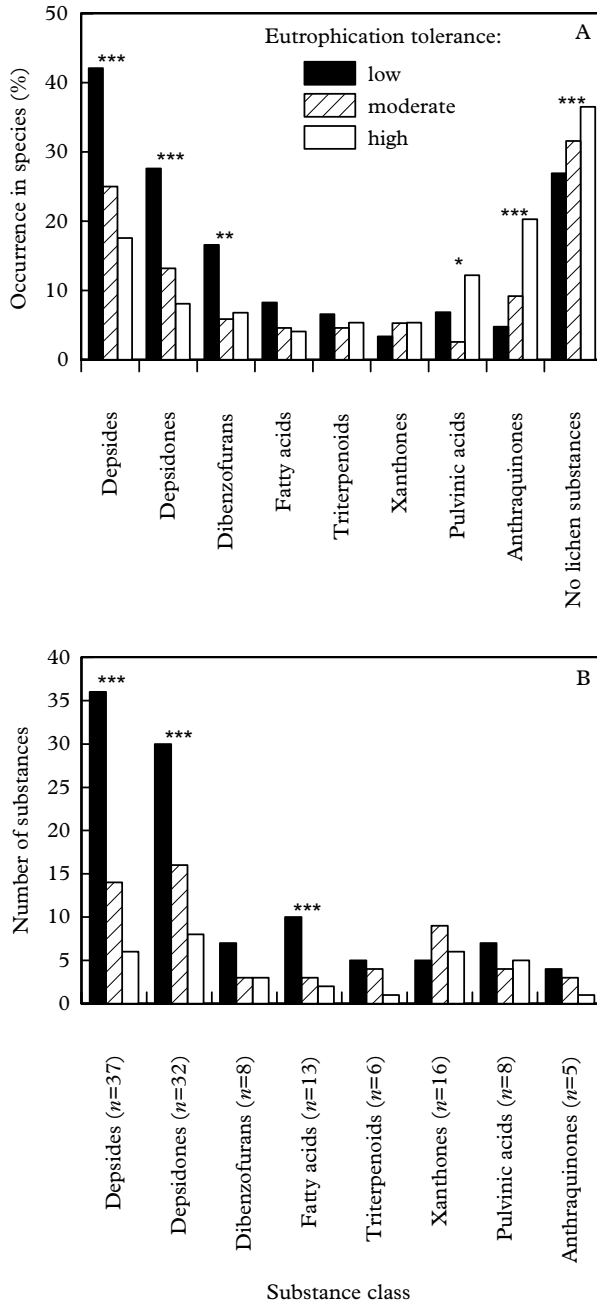


FIG. 1. A, frequency distribution of lichen substances belonging to selected substance classes among lichen species; B, number of lichen substances of different substance classes in lichen species with low, moderate or high eutrophication tolerance based on indicator values published by Wirth (2010). Asterisks indicate significant differences between levels of eutrophication tolerance (\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P \leq 0.001$ ).

37 depsides and 18 out of 32 depsidones are not known to be produced. Plotting the median of the number of lichen substances per family against the eutrophication tolerance indicator value shows a significant increase in anthraquinones (Fig. 2A) and a significant decrease in depsides (Fig. 2B), which becomes even more significant if members of the *Parmeliaceae* are removed (Fig. 2C).

### Case study of epiphytic lichens from the Netherlands

Depside and depsidones are found in approximately two-thirds of the eutrophication-sensitive lichens, but in only one-third (depsides;  $P = 0.06$ ) or none (depsidones;  $P < 0.001$ ) of the nitrophytes. While the depside atranorin occurs in lichen species irrespective of their tolerance to high nitrogen levels, six other depsides and all depsidones are limited to eutrophication-sensitive species (Table 3). Pulvinic acids lacking in the eutrophication-sensitive species occur in more than half of the eutrophication-tolerant species. The number of xanthones is higher in the sensitive than in the tolerant lichens, but this difference is merely due to one species (*Pyrrhospora quercea*) that produces three different xanthones. Therefore, the proportion of xanthone-producing species does not appear to differ between eutrophication-tolerant and -sensitive species.

### Discussion

Results of this study clearly show that lichen species tolerant or intolerant to high nitrogen concentrations differ in their secondary chemistry. Most depsides and depsidones, which form the largest groups of lichen substances (Huneck & Yoshimura 1996; Huneck 2001) are produced by species with low tolerance to eutrophication. The steep decline of chemical diversity in lichens between species tolerating low and moderate levels of eutrophication suggests that the reduction of chemical diversity caused by nitrogen pollution is not limited to a few

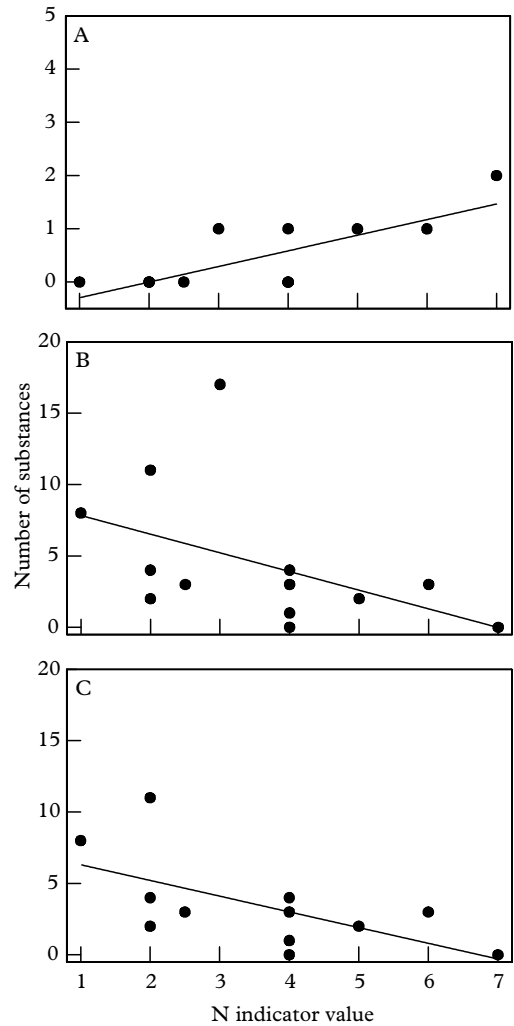


FIG. 2. Number of lichen substances found in species in 13 families with at least 10 species, arranged according to indicator values of Wirth (2010). Each datum point represents the median number of lichen substances produced by the species from the N tolerance category indicated. Data are plotted against median N indicator values of the families. A, anthraquinones ( $r = 0.77$ ,  $P = 0.001$ ); B, depsides ( $r = -0.47$ ,  $P = 0.05$ ); C, depsides without *Parmeliaceae* ( $r = -0.62$ ,  $P = 0.02$ ).

heavily polluted areas. Production of anthraquinones and pulvinic acids appears to be more widespread among eutrophication-tolerant lichens than sensitive species, but this cannot compensate for the loss of most other biochemical diversity with increasing

TABLE 2. Number of lichen substances found in species of the families with at least 10 species occurring in the analysis of Wirth's indicator values (Wirth 2010)

Family	N value		AN**	DE	DO	DI	FA	PU	TT	XA
	Median	IQ*								
<i>Cladoniaceae</i> (n = 33)	1	1	0	8	6	4	3	0	1	0
<i>Pilocarpaceae</i> (n = 11)	2	1	0	2	1	0	0	0	0	1
<i>Roccellaceae</i> (n = 16)	2	2	0	11	0	1	1	0	0	1
<i>Pertusariaceae</i> (n = 16)	2	1	0	4	7	0	1	0	0	3
<i>Stereocaulaceae</i> (n = 12)	2.5	2.5	0	3	5	1	4	0	1	0
<i>Parmeliaceae</i> (n = 74)	3	3	1	17	14	1	4	2	1	0
<i>Collemataceae</i> (n = 12)	4	2	0	0	0	0	0	0	0	0
<i>Verrucariaceae</i> (n = 18)	4	3.3	0	1	0	0	0	0	0	0
<i>Ramalinaceae</i> (n = 32)	4	4	0	4	6	1	0	0	0	0
<i>Peltigeraceae</i> (n = 16)	4	1	1	3	0	0	0	0	6	0
<i>Lecanoraceae</i> (n = 39)	5	3	1	2	5	4	4	2	1	12
<i>Physciaceae</i> (n = 45)	6	4	1	3	3	2	0	3	1	2
<i>Teloschistaceae</i> (n = 30)	7	2.8	2	0	2	0	0	0	0	0

\*IQ, interquartile range

\*\*AN, anthraquinones (n = 5); DE, depsides (n = 37); DO, depsidones (n = 32); DI, dibenzofurans (n = 8); FA, fatty acids (n = 13); PU, pulvinic acids (n = 8); TT, triterpenoids (n = 8); XA, xanthonones (n = 16).

TABLE 3. Total lichen substances of different substance classes in eutrophication-sensitive and eutrophication-tolerant epiphytic lichens recorded by van Dobben &amp; de Bakker (1996) in 1216 plots in the Netherlands

	Eutrophication-sensitive lichens	Eutrophication-tolerant lichens	Yates-corrected chi-square	P
Depsides	7	1	7.3	0.007
Depsidones	8	0	12.3	<0.001
Dibenzofurans	1	0	0.0	1.00
Fatty acids	1	0	0.0	1.00
Xanthonones	4	0	4.5	0.03
Triterpenoids	0	1	0.0	1.00
Anthraquinones	1	1	1.0	0.32
Pulvinic acids	0	3	2.7	0.10

nitrogen levels, as only relatively few anthraquinones and pulvinic acids are known. Many depsides, depsidones, dibenzofurans, fatty acids and other lichen substances are produced by only a few lichen species from nitrogen-poor sites, which suggests that even slight shifts in species diversity can cause substantial losses of biochemical diversity. The case study of epiphytic lichens from the Netherlands (van Dobben & de Bakker 1996) confirms this view.

The family-wide analysis shows that the trend for a loss of lichen substance diversity

with increasing eutrophication is not the result of the behaviour of a few species-rich lichen families, such as the predominantly eutrophication-sensitive *Parmeliaceae* or the mostly eutrophication-tolerant *Physciaceae* or *Teloschistaceae*. The absence of many lichen substances in the 13 largest families in the analysis implies that many substances are only found in families with a few species. This indicates that the reduced biochemical diversity due to eutrophication is a real diversity effect and not merely due to the individual traits of a few large families.

The mechanisms behind the relationship between eutrophication tolerance and secondary chemistry are not yet clear. Since lichen substances are known to influence the demands of lichens for the pH of their environment (i.e. the substratum and precipitation) (Hauck *et al.* 2009a, b), the increase of pH by the dissociation of ammonia in water may play a role in this relationship. Some depsides and depsidones and the dibenzofuran usnic acid were shown to be involved in the adaptation of lichens to acidity (Hauck & Jürgens 2008; Hauck *et al.* 2009a, 2010a). The pH-dependent metal complexation by lichen substances (Takani *et al.* 2002; Hauck *et al.* 2009b, 2010b) apparently influences the pH preferences of lichen species, probably as metal complexation is the initial step in the control of metal homeostasis by lichen substances (Hauck 2008; Hauck *et al.* 2009c). Usnic acid, for example, which was shown to promote the uptake of  $\text{Cu}^{2+}$  in *Evernia mesomorpha* and *Ramalina menziesii* (Hauck *et al.* 2009c), binds to this ion and other metals in the acidic range, whereas the anthraquinone parietin forms metal complexes under alkaline conditions (Takani *et al.* 2002; Hauck *et al.* 2009b). This difference would explain the increasing abundance of parietin along with increasing eutrophication tolerance.

This study indicates that changes in lichen frequency along nitrogen gradients take place not only among lichens that produce lichen substances but also lichens that do not produce them. A proposed mechanism for nitrogen tolerance both in vascular plants and lichens is the capability of species to provide sufficient carbon skeletons to assimilate ammonium into amino acids rapidly (Schortemeyer *et al.* 1997; Hauck & Wirth 2010), because of the high toxicity of free ammonium and ammonia (Neuhäuser *et al.* 2007). Since large amounts of carbohydrates are allocated to lichen substances in species producing such compounds, fewer carbohydrates can be expected to be available for ammonium assimilation in species with lichen substances than those without. This could explain the apparent tolerance to eutrophication of lichens without compounds. However, as many lichen species without

lichen substances are low-productive crustose lichens with thin thalli (Lakatos *et al.* 2006; Weber *et al.* 2007), not all lichens without lichen substances are tolerant to eutrophication (Hauck & Wirth 2010).

In conclusion, the present study can only show that there is some coincidence between the diversity of lichen substances and the nitrogen level of the environment. The high number of species (>500) and the large geographical scale (Central Europe) covered by the analysis suggest the existence of some causal link between the eutrophication tolerance and the biochemical diversity in lichens. Searching for mechanistic explanations, the possibility should be considered that the low biochemical diversity in lichens from nitrogen-rich environments and the known low biochemical diversity in nitrogen-fixing cyanolichens (Culberson 1969) with high intrathalline nitrogen concentrations (Nash 2008) might go back to similar (not yet known) causalities.

Prof. Dr. Volkmar Wirth is thanked for providing me with an electronic file of his indicator values published in Wirth (2010). Dr James D. Lawrey made valuable comments on the manuscript.

#### REFERENCES

- Culberson, C. F. (1969) *Chemical and Botanical Guide to Lichen Products*. Chapel Hill: University of North Carolina Press.
- Ellenberg, H. (1974) Zeigerwerte der Gefäßpflanzen Mitteleuropas. *Scripta Geobotanica* **9**: 1–97.
- Ellenberg, H. (1992) Zeigerwerte der Gefäßpflanzen Mitteleuropas (ohne *Rubus*). *Scripta Geobotanica* **18**: 9–166.
- Hauck, M. (2008) Metal homeostasis in *Hypogymnia physodes* is controlled by lichen substances. *Environmental Pollution* **153**: 304–308.
- Hauck, M. (2010) Ammonium and nitrate tolerance in lichens. *Environmental Pollution* **158**: 1127–1133.
- Hauck, M. & Jürgens, S.-R. (2008) Usnic acid controls the acidity tolerance of lichens. *Environmental Pollution* **156**: 115–122.
- Hauck, M. & Wirth, V. (2010) Preference of lichens for shady habitats is correlated with intolerance to high nitrogen levels. *Lichenologist* **42**: 475–484.
- Hauck, M., Jürgens, S.-R., Huneck, S. & Leuschner, C. (2009a) High acidity tolerance in lichens with fumarprotocetraric, perlatolic or thamnolic acids is correlated with low  $\text{pK}_{\text{a1}}$  values of these lichen substances. *Environmental Pollution* **157**: 2776–2780.
- Hauck, M., Jürgens, S.-R., Willenbruch, K., Huneck, S. & Leuschner, C. (2009b) Dissociation and metal-binding characteristics of yellow lichen substances

- suggest a relationship with site preferences of lichens. *Annals of Botany* **103**: 13–22.
- Hauck, M., Willenbruch, K. & Leuschner, C. (2009c) Lichen substances prevent lichens from nutrient deficiency. *Journal of Chemical Ecology* **35**: 71–73.
- Hauck, M., Jürgens, S.-R. & Leuschner, C. (2010a) Norstictic acid: correlations between its physico-chemical characteristics and ecological preferences of lichens producing this depsidone. *Environmental and Experimental Botany* **68**: 309–313.
- Hauck, M., Jürgens, S.-R. & Leuschner, C. (2010b) Effect of amino acid moieties on metal binding in pulvinic acid derivatives and ecological implications for lichens producing these compounds. *Bryologist* **113**: 1–7.
- Huneck, S. (2001) *New Results on the Chemistry of Lichen Substances*. Wien: Springer.
- Huneck, S. & Yoshimura, I. (1996) *Identification of Lichen Substances*. Berlin: Springer.
- Krupa, S. V. (2003) Effects of atmospheric ammonia (NH<sub>3</sub>) on terrestrial vegetation: a review. *Environmental Pollution* **124**: 179–221.
- Lakatos, M., Rascher, U. & Büdel, B. (2006) Functional characteristics of corticolous lichens in the understory of a tropical lowland rain forest. *New Phytologist* **172**: 679–695.
- Leuckert, C. (1985) Probleme der Flechten-Chemotaxonomie. Stoffkombinationen und ihre taxonomische Wertung. *Berichte der Deutschen Botanischen Gesellschaft* **98**: 401–408.
- Lumbsch, H. T. & Huhndorf, S. M. (2007) Outline of Ascomycota. *Mycotax* **13**: 1–58.
- Munzi, S., Pirintsos, S. A. & Loppi, S. (2009a) Chlorophyll degradation and inhibition of polyamine biosynthesis in the lichen *Xanthoria parietina* under nitrogen stress. *Ecotoxicology and Environmental Safety* **72**: 281–285.
- Munzi, S., Pisani, T. & Loppi, S. (2009b) The integrity of lichen cell membrane as a suitable parameter for monitoring biological effects of acute nitrogen pollution. *Ecotoxicology and Environmental Safety* **72**: 2009–2012.
- Nash, T. H. (2008) Nitrogen, its metabolism and potential contribution to ecosystems. In *Lichen Biology* (T. H. Nash, ed.): 216–233. Cambridge: Cambridge University Press.
- Neuhäuser, B., Dynowski, M., Mayer, M. & Ludewig, U. (2007) Regulation of NH<sub>4</sub><sup>+</sup> transport by essential cross talk between AMT monomers through the carboxyl tails. *Plant Physiology* **143**: 1651–1659.
- Olivier, J. G. J., Bouwman, A. F., van der Hook, K. W. & Berdowski, J. J. M. (1998) Global air emission inventories for anthropogenic sources of NO<sub>x</sub>, NH<sub>3</sub> and N<sub>2</sub>O in 1990. *Environmental Pollution* **102** (S1): 135–148.
- Pirintsos, S. A., Munzi, S., Loppi, S. & Kotzabasis, K. (2009) Do polyamines alter the sensitivity of lichens to nitrogen stress? *Ecotoxicology and Environmental Safety* **72**: 1331–1336.
- Riddell, J., Nash, T. H. & Padgett, P. (2008) The effect of HNO<sub>3</sub> gas on the lichen *Ramalina menziesii*. *Flora* **203**: 47–54.
- Schmull, M., Hauck, M., Vann, D. R., Johnson, A. H. & Runge, M. (2002) Site factors determining epiphytic lichen distribution in a dieback-affected spruce-fir forest on Whiteface Mountain, New York: stemflow chemistry. *Canadian Journal of Botany* **80**: 1131–1140.
- Schortemeyer, M., Stamp, P. & Feil, B. (1997) Ammonium tolerance and carbohydrate status in maize cultivars. *Annals of Botany* **79**: 25–30.
- Smith, C. W., Aptroot, A., Coppins, B. J., Fletcher, A., Gilbert, O. L., James, P. W. & Wolseley, P. A. (eds) (2009) *The Lichens of Great Britain and Ireland*. London: British Lichen Society.
- Søchting, U. (1997) Two major anthraquinone chemosyndromes in *Telochistaceae*. *Bibliotheca Lichenologica* **68**: 135–144.
- Sparrius, L. B. (2007) Response of epiphytic lichen communities to decreasing ammonia air concentrations in a moderately polluted area of the Netherlands. *Environmental Pollution* **146**: 375–379.
- Takani, M., Yajima, T., Masuda, H. & Yamauchi, O. (2002) Spectroscopic and structural characterization of copper(II) and palladium(II) complexes of a lichen substance usnic acid and its derivatives. Possible forms of environmental metals retained in lichens. *Journal of Inorganic Biochemistry* **91**: 139–150.
- van Dobben, H. F. & de Bakker, A. J. (1996) Remapping epiphytic lichen biodiversity in the Netherlands: effects of decreasing SO<sub>2</sub> and increasing NH<sub>3</sub>. *Acta Botanica Neerlandica* **45**: 55–71.
- van Dobben, H. F. & ter Braak, C. J. F. (1998) Effects of atmospheric NH<sub>3</sub> on epiphytic lichens in the the Netherlands: the pitfalls of biological monitoring. *Atmospheric Environment* **32**: 551–557.
- van Dobben, H. F. & ter Braak, C. J. F. (1999) Ranking of epiphytic lichen sensitivity to air pollution using survey data: a comparison of indicator scales. *Lichenologist* **31**: 27–39.
- van Herk, C. M. (1999) Mapping ammonia pollution with epiphytic lichens in the Netherlands. *Lichenologist* **31**: 9–20.
- Webb, J., Menzi, H., Pain, B. F., Misselbrook, T. H., Dämmgen, U., Hendriks, H. & Döhler, H. (2005) Managing ammonia emissions from livestock production in Europe. *Environmental Pollution* **135**: 399–406.
- Weber, B., Scherr, C., Reichenberger, H. & Büdel, B. (2007) Fast reactivation by high air humidity and photosynthetic performance of alpine lichens growing endolithically in limestone. *Arctic, Antarctic, and Alpine Research* **39**: 309–317.
- Wirth, V. (1995) *Die Flechten Baden-Württembergs*. Stuttgart: Ulmer.
- Wirth, V. (2010) Ökologische Zeigerwerte von Flechten – erweiterte und aktualisierte Fassung. *Herzogia* **23** (in press).

Accepted for publication 24 September 2010