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# Composition of Norway spruce litter and foliage in atmospherically acidified and nitrogen-saturated Bohemian Forest stands, Czech Republic

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We investigated litter fall and foliage chemistry in mature Norway spruce (*Picea abies*) stands in the catchments of Plešné (PL) and Čertovo (CT) lakes (Czech Republic). The stands differed in bedrock (granite in PL and mica-schist in CT) and soil chemistry, with lower base saturation (9% *vs*. 15%) and higher nitrogen saturation in the CT catchment. Concentrations and fluxes of ecologically important elements were measured for four years in six litter fall categories (needles, twigs, bark, lichen, cones, and "other material") at plots differing in elevation. Litter and foliage in the CT catchment had lower Ca concentrations and Ca:Al ratios, and higher N concentrations and N:Mg ratios, than in the PL catchment. These characteristics further progressed with elevation in both catchments, corresponding to higher acid and N deposition at higher elevation. As a result, concentrations of N, Al, and Fe were higher and concentrations of Ca and Mg, as well as Ca:Al and Mg:Al ratios were lower in most litter categories at high elevation (~1300 m) than at low elevation (~1100 m) plots.

## Introduction

The Bohemian Forest (Czech Republic) is one of the European lake districts most adversely affected by acidic deposition (Evans *et al*. 2001). Long-lasting high levels of atmospheric inputs of sulphur and nitrogen compounds resulted in the strong acidification of surface waters (Majer *et al*. 2003) and soils (Kopáček *et al*. 2002a, 2002b) in this mountainous ecosystem, causing nitrogen saturation (Kopáček *et al*. 2002c), and adversely affected the physiology of the spruce forests (Šantrůčková *et al*. 2007). Acidic deposition rapidly increased after 1950 and reached a maximum in the early 1980s (Majer *et al*. 2003). Between the mid-1980s and 2000, emission rates of $SO_2$, $NO_x$, and $NH_3$ decreased in the Czech Republic by ~87%, 51%, and 44%, respectively (Kopáček *et al*. 2002c). Despite a substantial decrease in acidic deposition, the Bohemian Forest soils and streams remain acidic, and an increase in soil base saturation is not expected within next several decades (Majer *et al*. 2003). Two of the Bohemian Forest lakes (Čertovo and Plešné) and their catchments have been the subject of integrated long-term research since the 1990s. The catchments are exposed to similar climatic conditions, but differ in bedrock and soil composition (base saturation), nitrogen saturation level, and soil ability to bind P. The catchment of Čertovo Lake has more acidic, N-saturated, and P accumulating soils, but the Plešné soils have net P losses and higher P leaching (Kaňa and Kopáček 2005, Kopáček *et al*. 2006a, 2006b). In addition, acidic and N depositions are higher at high than at low elevations of the catchments (Kopáček *et al*. 2006a, 2006b). These differences led us to ask the question: How are the different bedrock and soil conditions and differences in acidic deposition reflected in the spruce foliage and litter composition?

Nutrient concentrations in foliar litter have been shown to vary with climate and levels of forest stand pollution and fertilization (e.g. Berg and McClaugherty 2008, Jandl *et al*. 2002). In general, soil acidification and associated leaching of Mg, Ca, and K and elevated Al mobilisation are usually associated with less favourable nutritional status, whereas N deposition tends to increase the fertility of naturally N-limited terrestrial ecosystems (e.g. Puhe and Ulrich 2001). Shortages of base cations and elevated Al mobility in acidic soils influence litter composition, and are clearly indicated by reduced Ca:Al and Mg:Al ratios in soil solutions and foliage (e.g., Cronan and Grigal 1995). In contrast, elevated inputs of P, K, Ca, and Mg to forest ecosystems and increased availability of their soil pools usually increase their concentrations in foliage and litter. Changes in N availability and concentrations in litter cause changes in the concentrations of other nutrients that are structurally connected to N (Berg and Gerstberger 2004, Berg and McClaugherty 2008).

In concordance with these results, we hypothesised that there were differences in (1) foliage and litter composition between the Plešné and Čertovo catchments due to their different soil chemistry, and (2) along elevation gradients within these catchments due to the increasing atmospheric inputs of N and acidifying compounds with elevation in the Bohemian Forest. To test these hypotheses, we measured and evaluated chemical composition (C, N, P, Ca, Mg, Na, K, Al, Fe, and Mn) of foliage and six litter fall categories (needles, twigs, bark, lichen, cones, and "other material") in these catchments.

## Material and methods

### Study site description

The catchments of Plešné (PL) and Čertovo (CT) lakes are situated at elevations between 1030 and 1378 m a.s.l., and are north-east and east oriented, respectively. They differ in bedrock composition, with granite in the PL catchment and mica-schist (muscovitic gneiss) and quartzite in the CT catchment. Soils in both catchments are mostly leptosol, podsol, and dystric cambisol (Table 1); wetlands cover < 1% of the catchment areas. Soils are shallower (33 *vs*. 65 cm), but have higher base saturation (15% *vs*. 9%) in the PL than CT catchment (for more details *see* Table 1). The forests in the catchments are on average ~150 years old and are dominated by Norway spruce (*Picea abies*), with a minor contribution of European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). The average stand density and tree biomass are lower in the PL catchment, but the biomass of understory vegetation is higher than in the CT catchment (Table 1). Understory vegetation is dominated by bilberry (*Vaccinium myrtillus*; 86%) in the PL catchment and by bushgrass (*Calamagrostis villosa*; 42%) and bilberry (39%) in the CT catchment, with minor contributions of alpine lady fern (*Athyrium distentifolium*), greater woodrush (*Luzula sylvatica*), and wavy hair-grass (*Avenella flexuosa*) in both catchments (Svoboda *et al*. 2006a).

This study was conducted at three research plots in the PL catchment and two plots in the CT catchment. Two plots, one in each catchment, were situated at low elevations (PL-L: 48.7752°N, 13.8680°E, 1122 m a.s.l. and CT-L:

49.1627°N, 13.1993°E, 1057 m a.s.l.), whereas the other plots were at high elevations (CT-H (near the CT catchment summit): 49.1696°N, 13.1858°E, 1330 m a.s.l., PL-HS (south): 48.7700°N, 13.8630°E, 1310 m a.s.l., PL-HN (north): 48.7767°N, 13.8547°E, 1334 m a.s.l.).

In 2001–2007, the annual average air temperature varied between 4.1 and 5.9 °C, annual precipitation between 960 and 1981 mm, and snow cover usually lasted from November to late April. The average (± SD) throughfall deposition of S and total N was 25 ± 9 and 164 ± 50 mmol $m^{-2}$ $yr^{-1}$ (8 and 23 kg $ha^{-1}$ $yr^{-1}$), respectively, in the study catchments, with contributions of 30, 38, and 32% for $NH_4$-N, $NO_3$-N, and organic N to the total N pool (Kopáček *et al.* 2006a, 2006b). The S and N depositions were 20%–40% lower at the low *versus* high-elevation plots (Table 1). Despite similar N deposition to the catchments, nitrate leaching was higher from the CT than PL soils (98 *vs*. 82 mmol $m^{-2}$ $yr^{-1}$ on average) in 2000–2004, but nitrate leaching almost doubled from the PL catchment in 2005–2006 due to a partial forest damage caused by a bark beetle (*Ips typographus*) outbreak (Kopáček *et al*. 2006a, 2006b).

## Sampling and analyses

Litter was sampled using 5 quadratic frame traps (80 × 80 cm, height of 15 cm, bottom made of plastic sieve with porosity < 0.2 mm) situated at each plot beneath five representative trees

**Table 1**. Characteristics of study plots in the Bohemian Forest and respective throughfall deposition. Abbreviations: PL = Plešné Lake catchment; CT = Čertovo Lake catchment; L = low elevation; H = high elevation; HN = high elevation north.

| | PL-L | PL-HN | CT-L | CT-H |
|---|---|---|---|---|
| Throughfall[1)] | | | | |
| Amount (mm) | 1196 | 1586 | 1281 | 1555 |
| pH | 4.6 | 4.8 | 4.7 | 4.7 |
| N (mmol $m^{-2}$ $yr^{-1}$) | 152 | 190 | 148 | 201 |
| P (mmol $m^{-2}$ $yr^{-1}$) | 1.0 | 1.3 | 1.1 | 1.4 |
| S (mmol $m^{-2}$ $yr^{-1}$) | 21 | 27 | 21 | 35 |
| Ca (mmol $m^{-2}$ $yr^{-1}$) | 17 | 18 | 14 | 20 |
| Mg (mmol $m^{-2}$ $yr^{-1}$) | 6 | 8 | 6 | 8 |
| Soil[2)] | | | | |
| Depth (cm) | 33 | | 65 | |
| Amount (kg $m^{-2}$) | 92 | | 225 | |
| Type (% of catchment area) | dystric cambisol (27%), podsol (29%), leptosol (38%) | | dystric cambisol (58%), podsol (21%), leptosol (17%) | |
| ECEC (meq $kg^{-1}$) | 129 | | 104 | |
| Base saturation (%) | 15 | | 9 | |
| Exchangeable $Al^{3+}$ (%) | 57 | | 62 | |
| Exchangeable $H^+$ (%) | 28 | | 29 | |
| $pH_{CaCl2}$ | 2.5–4.4 | | 2.5–4.5 | |
| Stand density[3)] (trees $ha^{-1}$) | 155 | | 201 | |
| Tree dry biomass[3)] (t $ha^{-1}$) | 134 | | 173 | |
| Understory vegetation dry biomass[4)] (t $ha^{-1}$) | 12.1 | | 7.8 | |
| Bedrock | granite | | mica-schist and quartzite | |

[1)] Data on throughfall deposition are 2001–2007 means (Kopáček *et al.* 2006a, 2006b, J. Kopáček unpubl. data): N, total nitrogen ($NH_4$-N, $NO_3$-N, and organic N); P, total phosphorus; S, sulphate-sulphur; and Ca and Mg, ionic forms ($Ca^{2+}$ and $Mg^{2+}$). [2)] Average soil characteristics are based on 14 and 11 soil pits in the PL and CT catchment, respectively, excavated down to the bedrock (Kopáček *et al.* 2002a, 2002b). Amount is the average pool of dry weight < 2 mm soil fraction. ECEC, effective cation exchangeable capacity ($NH_4Cl$ and KCl extractable concentrations of $Ca^{2+}$, $Mg^{2+}$, $Na^+$, $K^+$, $Al^{3+}$, and $H^+$). One equivalent is one mole of charge. [3)] Forest characteristics were estimated on the basis of field measurements and an aerial orthophotograph from 2000 (Svoboda *et al.* 2006d, M. Svoboda unpubl. data). [4)] Data on average biomass (above and below ground) of understory vegetation are from Svoboda *et al.* (2006a).

(typical age, height, diameter, and crown status at the plot and surrounding area) from June 2003 to June 2007. Litter was collected three times per year, in spring after snowmelt at the upper plots (mostly at the end of May), in August, and in late October to early November. Litter from each trap was sampled individually and separated into the following six categories: needles, twigs, bark, lichen, cones, and "other material", i.e., remaining material, consisting mostly of poorly identifiable fragments. Beech leaves formed another category at CT-L, the only study plot, which had beech trees. Each fraction was dried at 50 °C for 12 hours. Samples from the August and autumn samplings were combined to obtain one sample representing the summer/autumn period. For chemical analyses, the dry samples of each category from all five traps were combined into one integrated sample for each plot, homogenised, and 2–5 g subsamples were finely ground for chemical analyses. Dry weight (DW) and ash content were estimated by drying samples at 105 °C for 2 hours, and combustion at 550 °C for 2 hours in an oven, respectively. Total P was determined by $HNO_3$ and $HClO_4$ digestion according to Kopáček *et al.* (2001). Total carbon (C) and nitrogen (N) were determined by a CN analyzer (NC 2100, ThermoQuest, Italy) according to Nelson and Sommers (1996). Total concentration of metals (Ca, Mg, Na, K, Al, Fe, and Mn) was determined by flame atomic absorption spectrometry after mineralization ($HNO_3$, $H_2SO_4$, and HF; 200 °C, 2 hours) in the accredited laboratory of the Czech Geological Survey, Prague. The original method (Emteryd 1989) was modified as follows: 1.0 g of sample was used instead of 0.4 g and $HClO_4$ was replaced with $H_2SO_4$. The average element concentrations reported in this study and the related uncertainty of determinations (in parentheses) were (mmol $kg^{-1}$): 44 050 (± 130) for C, 825 (± 10) for N, 22 (± 1.0) for P, 75 (± 6.9) for Ca, 16 (± 0.6) for Mg, 3 (± 0.5) for Na, 34 (± 1.5) for K, 17 (± 2.9) for Al, 6 (± 0.2) for Fe, and 4 (± 0.2) for Mn. All analyses were performed with samples dried at 50 °C, but chemical results further reported in this paper were recalculated per the DW mass at 105 °C.

Since 2004, the PL catchment has been subject to a bark beetle outbreak, leading to the ongoing death of trees. At the PL-HN plot, three of the five investigated trees died in August 2004 and the last two in summer 2006. Plot PL-L has been affected since summer 2006 and only one of the five investigated trees survived until the end of this study in spring 2007. Neither the PL-HS plot nor both CT plots were damaged by either bark beetle attacks or winds during our study.

Material for foliage analysis was collected by climbers from 5 representative trees (one representative branch from the bottom part of the upper third of the crown) at each plot in October 2001. The needles were separated into three age classes: current year needles (class 1), current + 1 year old needles (class 2), and current + 2 year old needles (class 3), dried at 50 °C for 12 hours, finely ground, and analyzed as described for litter (except for Mn). Foliage was not analyzed for Mn in 2001 and the average Mn concentrations used in this study are from Svoboda *et al.* (2006b), who analyzed foliage in the PL and CT catchments in 2003.

Chemical composition of other ecosystem compartments reported in this study was determined using the same methods and laboratories as litter and are from: Svoboda *et al.* (2006b, 2006c) for fine branches (diameter < 5 mm), branch bark, and stem bark; Svoboda *et al.* (2006a) for understory vegetation; and Kopáček *et al.* (2002a, 2002b) for the litter horizon (O) and the uppermost mineral soil horizon (A).

## Statistics

We used a Mann-Whitney *U*-test (Prism 5 for Windows, ver. 5.01) to test for differences in foliar and litter compositions between (i) the study catchments (PL-L plus PL-HS *versus* CT-L plus CT-H), number of observations ($n$) was 16 for each litter category in each catchment (8 samplings at each plot), and $n = 30$ for foliage in each catchment (5 samples of all 3 age classes at each plot); (ii) low and high elevation plots (PL-L plus CT-L *versus* PL-HS plus CT-H), with the same $n$ values for litter and foliage as above; and (iii) foliage age class 1 and 3, with $n = 15$ for both age classes in the PL catchment (PL-L, PL-HS, and PL-HN), and $n = 10$ in the CT catchment (CT-L and CT-H). A non-parametric procedure was selected because of non-homogeneous variances. Data on litter fall at the PL-HN plot were excluded from this test due to an effect of the bark beetle outbreak on litter composition.

Average concentrations of elements in total litter fall were calculated for each catchment, plot and sampling date as a mass-weighted mean ($C_{\mathrm{MWM}}$, mol kg$^{-1}$) for all litter categories as follows:

$$C_{\mathrm{MWM}} = \sum M_i C_i / \sum M_i \quad (1)$$

where $C_i$ is the element concentration (mol kg$^{-1}$) and $M_i$ is the dry mass (kg m$^{-2}$) of litter category $i$. Average composition of individual litter categories was the arithmetical mean for all samples at the CT-L and CT-H plots in the CT catchment, and for all three PL plots, excluding samples affected by the bark beetle attack (i.e., PL-HN since summer 2004 and PL-L since summer 2006), in the PL catchment.

## Results and discussion

### Foliage composition

In general, concentrations of P, Mg, and K decreased, whereas those of Ca, Na, Al, and Fe increased with needle age in both catchments (Table 2), and all these differences between age classes 1 and 3 were significant ($U$-test, $p < 0.05$). Such changes are typical for needle senescence and were similar to those recorded in Höglwald (Huber *et al.* 2004).

The average composition of spruce foliage in the Bohemian Forest (calculated for all plots and age categories) was within the range reported for Norway spruce forests in Europe (Table 3). The concentrations of Ca and Mg were lower and those of N were usually higher than at Scandinavian sites (e.g., Johansson 1995, Stefan *et al.* 1997, Luyssaert *et al.* 2005), which were less affected by acidic and N depositions than the Bohemian Forest, but were similar to the data reported from other central European sites (Stefan *et al.* 1997, Bauer *et al.* 2000, Huber *et al.* 2004, Oulehle *et al.* 2006) with similar levels and trends of air pollution (e.g., Schöpp *et al.* 2003). The composition of the Bohemian Forest

**Table 2**. Average (± SD) chemical composition of Norway spruce needles in the catchments of Plešné (PL) and Čertovo (CT) Lakes. Abbreviations: L, low elevation; H, high elevation; HS, high elevation-south; HN, high elevation-north. Number of observations, $n$ = 5 for each age class at each plot.

| | Age class | C (mol kg$^{-1}$) | N (mol kg$^{-1}$) | P (mmol kg$^{-1}$) | Ca (mmol kg$^{-1}$) | Mg (mmol kg$^{-1}$) | Na (mmol kg$^{-1}$) | K (mmol kg$^{-1}$) | Al (mmol kg$^{-1}$) | Fe (mmol kg$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| Plots$^{1)}$ | | | | | | | | | | |
| PL-L | 1,2,3 | 43.1 ± 0.2 | 0.95 ± 0.06 | 36 ± 7 | 85 ± 26 | 36 ± 6 | 1.3 ± 0.3 | 111 ± 23 | 1.7 ± 0.5 | 0.8 ± 0.2 |
| PL-HS | 1,2,3 | 43.1 ± 0.3 | 0.93 ± 0.08 | 39 ± 10 | 83 ± 26 | 32 ± 13 | 2.0 ± 1.3 | 89 ± 27 | 4.0 ± 1.4 | 1.4 ± 0.4 |
| PL-HN | 1,2,3 | 43.1 ± 0.2 | 1.00 ± 0.08 | 37 ± 9 | 75 ± 27 | 26 ± 9 | 1.9 ± 1.1 | 92 ± 15 | 2.7 ± 0.9 | 1.2 ± 0.3 |
| CT-L | 1,2,3 | 44.5 ± 0.4 | 1.05 ± 0.13 | 40 ± 12 | 74 ± 37 | 41 ± 22 | 2.5 ± 2.2 | 145 ± 40 | 2.5 ± 0.9 | 0.9 ± 0.2 |
| CT-H | 1,2,3 | 44.3 ± 0.8 | 1.07 ± 0.08 | 46 ± 10 | 73 ± 31 | 26 ± 6 | 1.9 ± 2.1 | 112 ± 21 | 3.4 ± 1.4 | 1.3 ± 0.5 |
| Needle age$^{2)}$ | | | | | | | | | | |
| PL-L,HS,HN | 1 | 43.1 ± 0.2 | 0.99 ± 0.09 | 46 ± 7 | 66 ± 18 | 36 ± 8 | 1.3 ± 0.5 | 111 ± 29 | 1.9 ± 0.8 | 0.9 ± 0.2 |
| PL-L,HS,HN | 2 | 43.2 ± 0.3 | 0.95 ± 0.07 | 34 ± 5 | 90 ± 27 | 32 ± 11 | 1.7 ± 0.6 | 90 ± 19 | 3.1 ± 1.2 | 1.2 ± 0.4 |
| PL-L,HS,HN | 3 | 43.1 ± 0.2 | 0.94 ± 0.07 | 32 ± 6 | 86 ± 28 | 26 ± 10 | 2.2 ± 1.4 | 92 ± 18 | 3.4 ± 1.5 | 1.3 ± 0.4 |
| CT-L,H | 1 | 44.2 ± 0.5 | 1.06 ± 0.10 | 52 ± 7 | 49 ± 21 | 39 ± 15 | 1.7 ± 1.6 | 156 ± 43 | 1.7 ± 0.3 | 0.8 ± 0.2 |
| CT-L,H | 2 | 44.3 ± 0.8 | 1.05 ± 0.12 | 41 ± 11 | 82 ± 33 | 35 ± 19 | 2.2 ± 2.1 | 119 ± 24 | 2.9 ± 0.8 | 1.2 ± 0.4 |
| CT-L,H | 3 | 44.6 ± 0.4 | 1.08 ± 0.11 | 37 ± 11 | 89 ± 34 | 28 ± 18 | 2.8 ± 2.6 | 111 ± 19 | 4.1 ± 1.1 | 1.4 ± 0.4 |

[1)] Average for needles of all age classes at the individual plots. [2)] Average for needles of the same age in the PL and CT catchments.

**Table 3**. The average composition of Norway spruce foliage in the Bohemian Forest and a comparison with selected European sites. ND = no data.

| Site | C (mol kg$^{-1}$) | N (mol kg$^{-1}$) | P (mmol kg$^{-1}$) | Ca (mmol kg$^{-1}$) | Mg (mmol kg$^{-1}$) | Na (mmol kg$^{-1}$) | K (mmol kg$^{-1}$) | Al (mmol kg$^{-1}$) | Fe (mmol kg$^{-1}$) | Mn (mmol kg$^{-1}$) | Molar ratio Ca:Al | Molar ratio N:Mg |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bohemian Forest[1] | 43.7 ± 0.8 | 1.01 ± 0.11 | 40 ± 10 | 78 ± 29 | 33 ± 14 | 2.0 ± 1.5 | 113 ± 33 | 2.8 ± 1.3 | 1.1 ± 0.4 | 10 ± 4.8 | 27 ± 15 | 31 ± 15 |
| Central Europe[2] | ND | 1.01 | 45 | 163 | 46 | 2.3 | 164 | 4.2 | 1.3 | 19 | 39 | 22 |
| Waldstein, Germany[3] | 42.2 | 1.06 | 54 | 156 | 23 | ND | 178 | ND | ND | ND | ND | 46 |
| Höglwald, Germany[4] | ND | 0.99 | 38 | 123 | 36 | ND | 78 | 3.4 | 1.3 | 54 | 36 | 28 |
| Načetín, Czech Rep.[5] | ND | 1.09 | 44 | 43 | 30 | 0.5 | 152 | 3.2 | ND | 8 | 13 | 36 |
| Finland[6] | ND | 0.80 | 46 | 131 | 49 | ND | 164 | 2.0 | 0.7 | 15 | 67 | 16 |
| Norway[7] | ND | 0.83 | 36 | 153 | 40 | 1.4 | 140 | 3.6 | 0.7 | 21 | 42 | 21 |

[1] Average (± SD) chemical composition of Norway spruce needles (three age classes) in five study plots (25 trees) in the Bohemian Forest. [2] Average for 150 plots in central Europe (Austria, Czech Republic, Germany, Slovakia) sampled in 1995 (Stefan *et al.* 1997). [3] Average for 1993–1997 period, 50°12´N, 11°53´E, elevation 700 m, age 142 yr (Bauer *et al.* 2000). [4] The 1993–1999 average for control plot in Höglwald, 48°17´N, 11°04´E, hilly landscape (Huber *et al.* 2004). [5] Average for 1993–1997 period, 50°35´N, 13°15´E, elevation 775 m, age 70 yr (Oulehle *et al.* 2006, Bauer *et al.* 2000). [6] Average for 13 plots in Finland sampled in 1995 (Stefan *et al.* 1997). [7] Average for 45 plots in southeastern Norway, mature trees at elevations > 550 m, sampled in 1995 (Stefan *et al.* 1997).

foliage exhibited similar characteristics indicating soil acidification (high Al concentrations, and low Ca:Al and Mg:Al ratios) as reported e.g., for Höglwald by Huber *et al*. (2004), with the exception of lower Mn concentrations. We assume that the lower Mn concentrations in the current Bohemian Forest foliage as compared with those recorded in Höglwald may indicate a greater extent of cumulative long-term acidic deposition and greater depletion of easily available soil Mn pools. High Mn concentration in foliage is a fingerprint of present-day acidification (Puhe and Ulrich 2001), because Mn is rapidly mobilized during early acidification stages. The difference between Mn concentrations in the CT and PL foliage is small (10.1 *vs*. 8.9 mmol kg$^{-1}$), despite almost 2-fold higher Mn concentrations in the CT than PL bedrock and soils (7.1 and 4.6 *vs*. 3.0 and 1.6 mmol kg$^{-1}$, respectively; Kopáček *et al*. 2002a, 2002b).

Our results on foliage composition are based on one sampling, and comparison with other sites should be done with caution. Spruce needle composition has been shown to reflect climatic parameters, especially extremely hot and dry summers, with particular effects on reductions in N, P, K, and Mg concentrations (Stefan and Gabler 1998). Nevertheless, the foliage sampling in the autumn of 2001 followed a climatically normal year in the Bohemian Forest, with no apparent extreme events like droughts, floods and frosts, and the average summer (June to September) temperature and precipitation were 0.3 °C and 4% lower than the 1961–2007 averages, respectively (Churáňov Station; Czech Hydrometeorological Institute). Climatic conditions for the 2001 sampling can thus be considered representative of the long-term average. From this point of view, chemical composition of the Bohemian Forest foliage (Table 3) did not show symptoms of insufficient nutrient supply for spruce as compared with the criteria given by Hüttl (1991), with threshold N, P, Ca, Mg, and K concentrations of 860, 35, 50, 30 and 100 mmol kg$^{-1}$, respectively, despite the long-lasting atmospheric acidification of catchment soils (Majer *et al*. 2003). The only exception was lower Mg concentration (26 mmol kg$^{-1}$) in two of the three high-elevation plots (PL-HN and CT-H; Table 2).

## Litter fall composition

The chemical composition of the litter categories was relatively uniform for C concentrations (40–45 mol kg$^{-1}$), but differed for all other elements. The highest N concentrations were observed in lichen and "other material" (1.5 and 1.4 mol kg$^{-1}$, respectively), and the lowest (0.5 mol kg$^{-1}$) was in cones, which typically (Gordon *et al.* 2000) had the lowest concentrations of most elements. Similar patterns, with maximum concentrations in "other material" and minimum in cones, were typical for P, Al, and Fe (Table 4). In contrast to Al and Fe, Mn concentrations were highest in needles and bark (5 and 3.5 mmol kg$^{-1}$, respectively). The distribution of individual base cations in the litter fall differed. Maximum and minimum Ca concentrations (188 and 5 mmol kg$^{-1}$) occurred in bark and cones, respectively. Mg concentrations varied within a narrower range, from 10 mmol kg$^{-1}$ in twigs to 27 mmol kg$^{-1}$ in "other material". K concentrations were lowest in twigs (17 mmol kg$^{-1}$) and highest in lichen and cones (54–68 mmol kg$^{-1}$). Na concentrations varied between 0.8 mmol kg$^{-1}$ in needles and 12.8 mmol kg$^{-1}$ in "other material".

The differences in element composition and annual fluxes of litter categories (Table 5) resulted in different contributions of the litter categories to the total elemental fluxes in the Bohemian Forest catchments (Table 6). Needle fall represented the dominant flux for Mn (69%); for C, N, P, Mg, and K (46%–52%) it was similar to the contribution of needles to the total mass flux of litter (47%). In contrast, the needle fall represented a minor flux for Na, Al, and Fe (10%–16%); their major fluxes were associated with "other material" (46%–49%). Twigs exhibited the lowest variation in their contribution to the total fluxes of individual elements (12%–26%), whereas the greatest variation was associated with cones, ranging from 1% for Ca to 20% for K (Table 6).

A comparison of litter chemistry with other ecosystem compartments that contribute most to the litter fall (foliage, fine branches, branch bark and stem bark), and/or result from the litter fall (litter soil horizon) is given in Table 4. Concentrations of C and Ca in litter needles, twigs, and bark were similar to those in foliage (average for all three age classes), fine branches, and bark of living trees, respectively. In contrast, litter had lower concentrations of nutrients (K, P, Mg, and Mn) and Na, while higher concentrations of Al and Fe. The highest depletion as compared with their concentrations in living tissue was observed for K (68%–83%), while that for P, Mg, Mn, and Na typically varied between 25% and 65%. The highest increase in Al and Fe concentrations occurred between litter bark and stem (or branch) bark of living trees (Table 4). The N concentrations did not behave consistently, being 20% and 30% lower in the litter needles and twigs than in foliage and fine branches of living trees, respectively, but 25%–50% higher in the litter bark than in branch and stem bark.

The differences in the composition of litter and corresponding compartments of living trees are in concordance with the decreasing concentration of P, Mg, and K and increasing concentrations of Al and Fe in aging needles (Table 2). Such a pattern reflects the translocation of nutrients from old to young tissue (e.g., Berg and McClaugherty 2008). Further differences in litter and living material composition could become more pronounced due to canopy leaching, which typically increases K, Mg, and Ca concentrations in throughfall as compared with deposition in treeless areas (e.g., Pedersen and Bille-Hansen 1999, Kopáček *et al.* 2009). Many studies have shown that the mobile element K is easily leached from litter and plant remains (e.g., Palviainen *et al.* 2004, Berg and McClaugherty 2008), and litter material is subjected to partial leaching during the residence time in the traps (Pedersen and Bille-Hansen 1999). Consequently, the long-lasting litter storage in traps (on average six months in winter and three in summer) during this study could partly underestimate litter fall fluxes of easily soluble metals like K, Mg, Mn, and Na, as observed elsewhere (Ukonmaanaho and Starr 2001).

Chemical composition of the total litter fall greatly differed from that of the soil litter horizon in both the catchments (Table 4). The soil litter horizon had lower concentrations of C, Ca, and Mn that were lost from the soil during litter decomposition. In contrast, concentrations of other elements were higher in the soil litter horizon than in litter, by 14%–44% for P, Mg,

**Table 4**. Comparison of the composition of litter fall (LF) with composition of foliage, fine branches, bark, above ground understory vegetation, and the upper soil horizons in the of Plešné (PL) and Čertovo (CT) catchments.

| | C (mol kg$^{-1}$) | N (mol kg$^{-1}$) | P (mmol kg$^{-1}$) | Ca (mmol kg$^{-1}$) | Mg (mmol kg$^{-1}$) | Na (mmol kg$^{-1}$) | K (mmol kg$^{-1}$) | Al (mmol kg$^{-1}$) | Fe (mmol kg$^{-1}$) | Mn (mmol kg$^{-1}$) | Molar ratio | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | C:N | Ca:Al |
| PL | | | | | | | | | | | | |
| Foliage | 43.1 | 0.96 | 37 | 81 | 31 | 1.7 | 97 | 2.8 | 1.1 | 8.9 | 45 | 29 |
| Fine branches | 44.2 | 1.01 | 45 | 77 | 33 | 5.0 | 97 | 15 | 4.8 | 5.7 | 44 | 5.1 |
| Branch bark | 42.0 | 0.58 | 26 | 219 | 41 | 4.5 | 71 | 8.2 | 2.5 | 9.1 | 73 | 27 |
| Stem bark | 42.8 | 0.43 | 18 | 199 | 35 | 3.7 | 68 | 1.9 | 0.7 | 9.0 | 99 | 103 |
| Understory veg. | 42.5 | 0.81 | 31 | 107 | 37 | 0.8 | 132 | 6.8 | 1.6 | 10 | 53 | 16 |
| O-horizon* | 40.9 | 1.41 | 30(7) | 60(48) | 18(8) | 30(4) | 57(11) | 200(11) | 49 | 2.3 | 29 | 0.3 |
| A-horizon* | 23.6 | 0.96 | 23(6) | 37(15) | 27(4) | 257(2) | 420(5) | 1200(26) | 86 | 2.2 | 25 | 0.02 |
| LF-total | 43.9 | 0.83 | 22 | 87 | 17 | 2.7 | 33 | 19 | 6.6 | 3.9 | 53 | 4.6 |
| LF-needle | 44.0 | 0.79 | 23 | 88 | 17 | 0.8 | 33 | 3.9 | 1.2 | 5.4 | 56 | 23 |
| LF-twigs | 44.8 | 0.67 | 17 | 74 | 12 | 2.2 | 19 | 19 | 6.8 | 2.2 | 67 | 3.8 |
| LF-bark | 43.4 | 0.77 | 16 | 188 | 16 | 3.5 | 21 | 31 | 11 | 3.6 | 56 | 6.1 |
| LF-lichen | 40.4 | 1.51 | 22 | 82 | 23 | 4.6 | 68 | 36 | 13 | 2.2 | 27 | 2.3 |
| LF-cone | 44.4 | 0.50 | 15 | 6.7 | 19 | 1.8 | 54 | 2.2 | 0.6 | 0.7 | 89 | 3.0 |
| LF-other | 42.9 | 1.47 | 41 | 86 | 27 | 13 | 49 | 79 | 28 | 3.5 | 29 | 1.1 |
| CT | | | | | | | | | | | | |
| Foliage | 44.4 | 1.06 | 43 | 73 | 34 | 2.2 | 128 | 2.9 | 1.1 | 10 | 42 | 25 |
| Fine branches | 44.4 | 0.99 | 43 | 67 | 29 | 4.4 | 116 | 11 | 3.3 | 4.4 | 45 | 6.1 |
| Branch bark | 42.2 | 0.57 | 23 | 185 | 39 | 3.3 | 65 | 8.4 | 2.1 | 9.5 | 74 | 22 |
| Stem bark | 43.0 | 0.43 | 20 | 188 | 38 | 4.0 | 75 | 3.1 | 0.7 | 11 | 101 | 60 |
| Understory veg. | 41.4 | 1.07 | 40 | 70 | 37 | 0.6 | 238 | 4.8 | 1.7 | 11 | 39 | 14 |
| O-horizon* | 41.1 | 1.60 | 34(8) | 50(37) | 28(10) | 31(4) | 61(16) | 260(15) | 102 | 3.2 | 26 | 0.2 |
| A-horizon* | 25.6 | 1.03 | 34(11) | 30(10) | 56(4) | 139(3) | 242(7) | 1470(38) | 241 | 3.6 | 25 | 0.04 |
| LF-total | 44.2 | 0.82 | 22 | 63 | 15 | 2.7 | 34 | 15 | 5.1 | 3.3 | 54 | 4.2 |
| LF-needle | 44.3 | 0.82 | 23 | 69 | 15 | 1.1 | 32 | 4.7 | 1.3 | 4.5 | 54 | 15 |
| LF-twigs | 44.8 | 0.71 | 16 | 65 | 10 | 2.2 | 17 | 18 | 6.1 | 2.0 | 63 | 3.7 |
| LF-bark | 43.9 | 0.89 | 19 | 150 | 15 | 3.2 | 20 | 31 | 11 | 3.5 | 49 | 4.9 |
| LF-lichen | 40.7 | 1.50 | 25 | 86 | 23 | 4.8 | 65 | 39 | 14 | 2.4 | 27 | 2.2 |
| LF-cone | 44.5 | 0.50 | 18 | 5.2 | 20 | 2.1 | 64 | 2.0 | 0.5 | 0.7 | 89 | 2.6 |
| LF-other | 43.5 | 1.42 | 43 | 62 | 24 | 13 | 45 | 75 | 28 | 2.9 | 31 | 0.8 |
| LF-beech leaf | 43.9 | 1.10 | 28 | 53 | 23 | 2.7 | 58 | 9.2 | 4.3 | 3.0 | 40 | 5.8 |

* Numbers in parenthesis are concentrations of $NH_4Cl$ extractable base cations and Al, and oxalate extractable P (Kopáček *et al.* 2002a, 2002b).

**Table 5**. Average (± SD) fluxes and chemical composition of litter in the catchments of Plešné (PL) and Čertovo (CT) lakes. Abbreviations: DW, dry weight; L, low elevation; H, high elevation; HS, high elevation-south. Number of observations, *n* = 8 for each plot.

| | | DW (kg ha$^{-1}$ d$^{-1}$) | C (mol kg$^{-1}$) | N (mol kg$^{-1}$) | P (mmol kg$^{-1}$) | Ca (mmol kg$^{-1}$) | Mg (mmol kg$^{-1}$) | Na (mmol kg$^{-1}$) | K (mmol kg$^{-1}$) | Al (mmol kg$^{-1}$) | Fe (mmol kg$^{-1}$) | Mn (mmol kg$^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Needles | PL-L | 11 ± 14 | 43.9 ± 0.5 | 0.73 ± 0.06 | 22 ± 4 | 88 ± 8 | 17 ± 3 | 0.7 ± 0.3 | 37 ± 12 | 3.1 ± 0.5 | 1.0 ± 0.1 | 3.9 ± 0.5 |
| | PL-HS | 6.3 ± 1.6 | 44.0 ± 0.4 | 0.82 ± 0.08 | 24 ± 3 | 88 ± 6 | 17 ± 3 | 0.9 ± 0.4 | 28 ± 4 | 4.7 ± 0.9 | 1.4 ± 0.3 | 6.8 ± 0.9 |
| | CT-L | 4.6 ± 1.1 | 44.2 ± 0.7 | 0.78 ± 0.10 | 19 ± 2 | 69 ± 4 | 17 ± 1 | 1.0 ± 0.5 | 31 ± 8 | 4.3 ± 0.4 | 1.1 ± 0.1 | 4.4 ± 0.4 |
| | CT-H | 5.6 ± 1.8 | 44.3 ± 0.5 | 0.85 ± 0.10 | 27 ± 2 | 68 ± 5 | 13 ± 1 | 1.2 ± 0.4 | 33 ± 5 | 5.0 ± 0.6 | 1.5 ± 0.2 | 4.6 ± 0.5 |
| Twigs | PL-L | 3.0 ± 2.7 | 44.9 ± 1.1 | 0.68 ± 0.90 | 18 ± 3 | 82 ± 8 | 13 ± 4 | 2.3 ± 0.5 | 22 ± 8 | 18 ± 4 | 6.5 ± 1.4 | 2.0 ± 0.4 |
| | PL-HS | 5.2 ± 3.6 | 44.6 ± 0.6 | 0.66 ± 0.07 | 16 ± 2 | 70 ± 8 | 12 ± 4 | 2.2 ± 0.4 | 16 ± 2 | 20 ± 4 | 6.7 ± 1.1 | 2.4 ± 0.1 |
| | CT-L | 2.0 ± 1.6 | 44.8 ± 1.0 | 0.67 ± 0.12 | 15 ± 1 | 70 ± 5 | 11 ± 1 | 1.9 ± 0.5 | 17 ± 2 | 15 ± 2 | 5.4 ± 0.7 | 2.1 ± 0.4 |
| | CT-H | 1.9 ± 1.2 | 44.8 ± 0.6 | 0.75 ± 0.10 | 18 ± 3 | 60 ± 4 | 9 ± 1 | 2.6 ± 0.8 | 17 ± 3 | 21 ± 4 | 6.9 ± 1.4 | 1.9 ± 0.3 |
| Bark | PL-L | 1.3 ± 1.1 | 43.5 ± 0.7 | 0.69 ± 0.07 | 15 ± 3 | 213 ± 24 | 16 ± 4 | 3.2 ± 0.9 | 20 ± 4 | 28 ± 3 | 10 ± 0.6 | 3.3 ± 0.9 |
| | PL-HS | 0.8 ± 0.2 | 43.4 ± 0.4 | 0.87 ± 0.15 | 18 ± 3 | 173 ± 28 | 16 ± 3 | 4.2 ± 1.0 | 22 ± 3 | 36 ± 7 | 13 ± 2.6 | 4.0 ± 0.4 |
| | CT-L | 0.4 ± 0.1 | 43.6 ± 0.6 | 0.90 ± 0.09 | 18 ± 3 | 176 ± 20 | 17 ± 2 | 3.0 ± 0.4 | 20 ± 3 | 28 ± 6 | 11 ± 1.3 | 3.9 ± 0.3 |
| | CT-H | 0.4 ± 0.2 | 44.2 ± 0.7 | 0.89 ± 0.09 | 19 ± 3 | 124 ± 12 | 14 ± 1 | 3.5 ± 0.8 | 20 ± 3 | 34 ± 7 | 12 ± 2.3 | 3.2 ± 0.3 |
| Lichen | PL-L | 0.29 ± 0.07 | 40.3 ± 0.5 | 1.55 ± 0.12 | 23 ± 2 | 83 ± 29 | 24 ± 3 | 4.0 ± 0.7 | 74 ± 10 | 31 ± 3 | 11 ± 1.3 | 1.8 ± 0.3 |
| | PL-HS | 0.46 ± 0.19 | 40.4 ± 0.2 | 1.48 ± 0.10 | 22 ± 2 | 90 ± 21 | 24 ± 3 | 5.3 ± 0.9 | 64 ± 4 | 40 ± 9 | 15 ± 2.6 | 2.7 ± 0.6 |
| | CT-L | 0.10 ± 0.05 | 40.6 ± 0.4 | 1.47 ± 0.13 | 24 ± 3 | 106 ± 21 | 25 ± 2 | 4.2 ± 1.0 | 63 ± 4 | 32 ± 3 | 12 ± 0.8 | 2.7 ± 0.6 |
| | CT-H | 0.13 ± 0.06 | 40.8 ± 0.5 | 1.53 ± 0.1 | 26 ± 3 | 65 ± 11 | 21 ± 1 | 5.4 ± 1.0 | 68 ± 3 | 45 ± 8 | 16 ± 2.4 | 2.1 ± 0.3 |
| Cones | PL-L | 1.4 ± 1.3 | 44.3 ± 1.0 | 0.46 ± 0.35 | 13 ± 11 | 5.9 ± 3.2 | 19 ± 14 | 1.6 ± 0.9 | 60 ± 14 | 2.0 ± 0.8 | 0.6 ± 0.3 | 0.6 ± 0.4 |
| | PL-HS | 1.4 ± 0.7 | 44.6 ± 1.2 | 0.55 ± 0.34 | 17 ± 14 | 6.8 ± 3.0 | 21 ± 9 | 2.0 ± 1.7 | 59 ± 18 | 2.0 ± 0.7 | 0.5 ± 0.2 | 0.9 ± 0.5 |
| | CT-L | 2.2 ± 1.9 | 44.7 ± 1.6 | 0.50 ± 0.27 | 15 ± 9 | 4.4 ± 1.2 | 22 ± 13 | 2.1 ± 1.9 | 73 ± 32 | 1.6 ± 0.3 | 0.4 ± 0.2 | 0.7 ± 0.4 |
| | CT-H | 1.3 ± 1.2 | 44.4 ± 0.9 | 0.50 ± 0.10 | 20 ± 8 | 5.7 ± 2.9 | 18 ± 5 | 2.0 ± 1.3 | 57 ± 34 | 2.3 ± 0.8 | 0.6 ± 0.2 | 0.8 ± 0.2 |
| Other | PL-L | 1.5 ± 0.7 | 43.1 ± 0.9 | 1.39 ± 0.16 | 40 ± 4 | 91 ± 20 | 27 ± 8 | 14 ± 6 | 51 ± 11 | 73 ± 22 | 25 ± 9 | 3.1 ± 0.9 |
| | PL-HS | 1.8 ± 0.6 | 42.7 ± 0.5 | 1.55 ± 0.11 | 42 ± 6 | 85 ± 14 | 29 ± 6 | 12 ± 2 | 49 ± 5 | 84 ± 22 | 30 ± 9 | 4.0 ± 0.6 |
| | CT-L | 1.0 ± 0.4 | 43.7 ± 0.8 | 1.33 ± 0.16 | 38 ± 6 | 68 ± 7 | 23 ± 4 | 10 ± 3 | 41 ± 8 | 61 ± 22 | 22 ± 9 | 2.9 ± 0.4 |
| | CT-H | 0.9 ± 0.3 | 43.3 ± 0.7 | 1.52 ± 0.13 | 49 ± 8 | 57 ± 6 | 24 ± 6 | 15 ± 8 | 48 ± 8 | 90 ± 33 | 33 ± 15 | 2.8 ± 0.4 |

**Table 6**. Annual element fluxes of litter fall in the Bohemian Forest (average ± SD for five plots in the 2003–2007 period, excluding samples affected by bark beetle attack) and the average relative contribution of individual litter categories to these fluxes (excluding beech leaves). DW = dry weight of litter fall.

| | DW | C | N | P | Ca | Mg | Na | K | Al | Fe | Mn |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total litter fall | | | | | | | | | | | |
| kg ha$^{-1}$ yr$^{-1}$ | 4529 ± 1545 | 2420 ± 811 | 51 ± 18 | 3.1 ± 1.0 | 13 ± 5.6 | 1.7 ± 0.6 | 0.3 ± 0.1 | 5.7 ± 1.6 | 2.1 ± 1.2 | 1.5 ± 0.9 | 0.9 ± 0.4 |
| mmol m$^{-2}$ yr$^{-1}$ | | 20170 | 367 | 10 | 33 | 7.1 | 1.2 | 15 | 7.7 | 2.7 | 1.6 |
| Contribution (%) | | | | | | | | | | | |
| Needles | 47 | 47 | 47 | 50 | 52 | 47 | 16 | 46 | 12 | 10 | 69 |
| Twigs | 24 | 24 | 20 | 18 | 22 | 16 | 19 | 12 | 26 | 26 | 14 |
| Bark | 5 | 5 | 5 | 4 | 12 | 5 | 7 | 3 | 9 | 9 | 5 |
| Lichen | 2 | 2 | 3 | 2 | 2 | 3 | 3 | 4 | 4 | 4 | 1 |
| Cones | 12 | 12 | 6 | 7 | 1 | 13 | 9 | 20 | 1 | 1 | 2 |
| Other | 10 | 10 | 18 | 19 | 10 | 16 | 46 | 14 | 48 | 49 | 9 |

and K, 42%–49% for N, and 89%–95% for Na, Al, and Fe. The respective values of molar C:N and C:P ratios of 53–54 and 1970 in the litter fall were higher than in the litter horizon (26–29 and 1290). Berg and McClaugherty (2008) summarised common changes occurring in element concentrations during litter decomposition. Most of the differences between the Bohemian Forest litter and soil litter horizon composition follow these general patterns that accompany litter mass loss, with increasing N, P, and Mg concentrations, most rapidly increasing concentrations of heavy metals, and decreasing Ca and Mn concentrations.

## Between-catchment differences in the foliage and litter fall composition

The chemical composition of foliage, litter fall, and other ecosystem compartments differed between the CT and PL catchments (Table 4). The foliage in CT had significantly higher (Table 7) concentrations of C, N, P, and K than the foliage in PL (Table 2). Similarly to foliage, most of litter categories had higher C concentrations in the CT catchment (Table 4). Even though the between-catchment differences in C concentrations were small in absolute values (< 0.6 mmol kg$^{-1}$), they were mostly significant (Table 7) and resulted from a significantly lower content of ash in all litter samples (except for lichen) collected in CT ($U$-test: $p < 0.05$). The respective concentrations of C and ash in the CT and PL total litter fall were 44.2 and 43.9 mmol kg$^{-1}$ and 2.1% and 2.7%, resulting in almost identical C concentrations of 45.14 and 45.13 mmol kg$^{-1}$ for the ash-free organic matter. The higher ash content of the litter in PL well corresponds to the higher concentrations of Ca in almost all litter fall categories (Table 7), as well as in other ecosystem compartments, including branches and bark of living trees, understory vegetation and soils (Table 4). The higher Ca availability in the PL environment primarily results from higher Ca concentrations in granite than mica-schist (112 *vs*. 52 mmol kg$^{-1}$), the dominant bedrocks of the PL and CT catchments, respectively (Kopáček *et al*. 2002a, 2002b), because atmospheric Ca deposition is similar in both catchments (Table 1).

The between-catchment difference in Ca concentrations was responsible for the higher Ca:Al ratios in most of the PL ecosystem compartments, because Al concentrations did not exhibit any consistent between-catchment differences (Table 4). In contrast to Ca, there were no consistent between-catchments differences in concentrations of other base cations in foliage and litter fall (Table 7), even though Mg concentrations were almost 2-fold higher in the CT than in the PL soils (Table 4) and 6-fold higher in the CT than in the PL bedrock (Kopáček *et al*. 2002a, 2002b).

Concentrations of N were higher in foliage, most litter fall categories, and the soil litter horizon in the CT than in the PL catchment (Table 4). Even though a part of this difference is associated with different ash contents, as in the case of C, the associated lower C:N ratios (Table 4) and higher molar N:Mg ratios (e.g., 54 *vs*. 47 for litter needle and 53 *vs*. 48 for total litter fall) in the CT than in the PL catchment indicate a higher N availability in the more N-saturated CT catchment. Similarly to the data of Huber *et al*. (2004) and Alewell *et al*. (2000), we observed a decrease in N concentrations with needle age, from 0.99 to 0.94 mol kg$^{-1}$ in needle classes 1 and 3, respectively, in the PL catchment (Table 2). In contrast, N concentrations were similar in classes 1 and 3 in the CT catchment, with averages of 1.06 and 1.08 mol kg$^{-1}$, respectively. In addition to the greater nitrate leaching from the CT than the PL soils (Kopáček *et al*. 2006a, 2006b) and the lower C:N ratio and higher N concentrations in the CT foliage, the absence of decreasing N concentrations during needle senescence could probably represent another symptom of the more progressed N-saturation of the CT catchment.

## Effect of elevation on the foliage and litter fall composition

Concentrations of Al and Fe in foliage were significantly higher and those of Mg and K significantly lower in the high- as compared with those in the low-elevation plots in the Bohemian Forest catchments (Table 7). Other elements did not exhibit significant differences (Table 7), even though the average concentrations of Ca were

**Table 7**. Significance (Mann-Whitney *U*-test, values given) of the differences in chemical composition of foliage and litter fall (LF) between Plešné and Čertovo catchments (PL *vs*. CT) and between low and high elevation plots in the Bohemian Forest (L *vs*. H). NS = not significant; *, < 0.05; **, < 0.01; ***, < 0.001. ND, not determined.

| | C | N | P | Ca | Mg | Na | K | Al | Fe | Mn | C:N | Ca:Al | Mg:Al |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PL *vs*. CT[1] | | | | | | | | | | | | | |
| Foliage[3] | 61*** | 202*** | 304* | NS | NS | NS | 237** | NS | NS | ND | 268** | 314* | NS |
| LF-needle | 64* | NS | NS | 1*** | NS | 64* | NS | 62* | NS | NS | NS | 15*** | 57** |
| LF-twigs | NS | NS | NS | 52** | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| LF-bark | 75.5* | 51* | NS | 45** | NS | NS | NS | NS | NS | NS | 53* | NS | NS |
| LF-lichen | NS | NS | 58.5** | NS | NS | NS | NS | NS | NS | NS | NS | NS | NS |
| LF-other | 65.5* | NS | NS | 13*** | NS | NS | 65.5* | NS | NS | 65.5* | NS | NS | NS |
| L *vs*. H[2] | | | | | | | | | | | | | |
| Foliage[3] | NS | NS | NS | NS | 245** | NS | 262** | 147** | 135*** | ND | NS | 178*** | 151*** |
| LF-needle | NS | 60* | 38*** | NS | 73* | NS | NS | 37*** | 11*** | 32*** | 56** | 63* | 39*** |
| LF-twigs | NS | NS | NS | 44** | 64* | NS | NS | 65* | 70* | NS | NS | 22*** | 46** |
| LF-bark | NS | NS | NS | 40*** | NS | 63* | NS | 51** | 36** | NS | NS | 35*** | 44*** |
| LF-lichen | NS | NS | NS | NS | NS | 31*** | NS | 16*** | 8.5*** | NS | NS | 45** | 30.5*** |
| LF-other | NS | 42.5** | 53** | NS | NS | NS | NS | NS | NS | NS | 49.5** | 68.5* | NS |

[1] Relationship between PL-L plus PL-HS and CT-L plus CT-H, *n* =16 for all the PL and CT litter categories (df = 30) and *n* = 30 for both PL and CT foliage (df = 58). [2] Relationship between PL-L plus CT-L and PL-HS plus CT-H, *n* and df values are the same as above for both litter and foliage. [3] Foliage includes needles of all age classes (1–3).

generally higher in the low-elevation plots, and the foliage and litter fall of the high-elevation plots were richer in P and N (Tables 2 and 5). All litter categories (except for "other material") had significantly higher concentrations of Al and Fe at high elevation plots (Table 7), while generally lower Ca and Mg concentrations (Table 5). This resulted in lower Ca:Al and Mg:Al ratios in all litter categories (as well as in foliage) at the high elevation plots (Table 7). In contrast, molar N:Mg ratios were generally higher in the high- than in the low-elevation plots; e.g., 36 *vs*. 26 in foliage and 57 *vs*. 45 in litter needles.

Decreasing Ca:Al and Mg:Al ratios and increasing N:Mg ratios are usually considered to be a fingerprint of elevated N inputs to N-limited coniferous forests and for high acidic deposition (e.g., Luyssaert *et al*. 2005). Acidic deposition leads to depletion of base-cation pools in soils and mobilization of Al and Fe (Norton and Veselý 2004). This process was in part mitigated by the relatively high Ca and Mg depositions associated with dust production from coal combustion until the 1980s. After the decline in emissions of particulates in central Europe (> 80% during the 1980–2000 period; Kopáček *et al*. 2002c), the deposition of base cations significantly declined as well (e.g., Hedin *et al*. 1994) being accompanied by decreasing Ca and Mg concentrations in foliage and litter (Alewell *et al*. 2000, Oulehle *et al*. 2006, Jandl *et al*. 2007). Almost simultaneously, acidic deposition declined in central Europe, leading to decreasing litter concentrations of S and Al (Alewell *et al*. 2000, Oulehle *et al*. 2006). The high-elevation plots in the Bohemian Forest were sampled relatively long time after the major decline in particulate emissions. Lower concentrations of Ca and Mg and higher concentrations of Al and Fe in the high-elevation litter thus probably reflect the long-term cumulative effect of acidic deposition on forest soils. Moreover, in the Bohemian Forests the high-elevation soil layer is thinner as compared with that at low elevations; the soil layer thickness decreases on average 9 cm per 100 m of elevation between 1050 and 1350 m (Kopáček *et al*. 2002a, 2002b). Thinner soil layer and higher cumulative acidic deposition probably caused lower fertility at high elevation plots and the observed differences in foliage and litter composition.

The higher concentrations of N and P in litter fall (Table 5), and especially in needles and "other material" (Table 7), at the high elevation plots most probably resulted from higher atmospheric inputs of these nutrients (Table 1). The higher element deposition at the higher elevations was due predominantly to higher precipitation amounts there (Table 1), because throughfall composition was similar at all the Bohemian Forest plots (Kopáček *et al*. 2006a, 2006b).

## Conclusions

Our results were in good concordance with the working hypothesis, predicting differences in the litter and foliage compositions between the study catchments and along the elevation gradients. The chemical composition of litter fall in the Bohemian Forest was typical for areas exposed to long-term acidic deposition and N-saturation, with low Ca, Mg, and Mn concentrations and low Ca:Al and Mg:Al ratios, but high N concentrations and N:Mg ratios. This was more pronounced at the high elevations, corresponding to the higher acidic deposition and shallower soils in these parts of the study catchments. In addition, the litter Al and Fe concentrations were higher at the high-elevation plots. Despite these adverse effects of chronic acidic deposition, chemical composition of the Bohemian Forest foliage (Table 3) did not show symptoms of insufficient nutrient supply for spruce according to criteria given by Hüttl (1991), with the exception of Mg at two of the five study plots.

The between-catchment differences in soil and bedrock chemistry in the PL and CT catchments were in part reflected in the foliage and litter composition. Higher base saturation (and Ca concentrations) in the PL soils resulted in higher mineral (ash) and Ca content and higher Ca:Al ratios in the PL foliage and litter. Similarly, the higher level of N-saturation in the CT catchment caused higher N concentrations and N:Mg ratios, while lower C:N ratios in a majority of the CT ecosystem compartments.

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