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Long-term ecological research of glacial lakes in the Bohemian Forest and their catchments

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Abstract

Glacial lakes in the Bohemian Forest (Šumava, Böhmerwald) belong to the most atmospherically acidified lake districts in the world. Available historical data and regular monitoring (since 1984) provide a valuable background for long-term ecological research of the catchment–lake ecosystems. This paper is an overview of recent projects covering the last two decades. The review of published papers provides details on the organization and aims of present research on the Bohemian Forest lakes that currently focuses on chemical and biological recovery of the catchment–lake systems from atmospheric acidification, and effects of climate change and forest vigour on biogeochemical processes in terrestrial and aquatic ecosystems.

Key words: atmospheric acidification, biological recovery, nutrients, soil, water, forest dieback

Introduction

The Bohemian Forest lakes have attracted explorers for more than one hundred years. Early hydrobiological research, starting more than 140 years ago (Frič 1872, 1874), sporadic research before the 1980s, and palaeolimnological studies provided a valuable background for long-term ecological research of the Bohemian Forest lake ecosystems (for review, see Veselý 1994, Vrba et al. 2000, 2003a, Kopáček & Vrba 2006, Soldán et al. 2012).

The regular monitoring of the Bohemian Forest lakes was initiated in 1984 and showed that the Bohemian Forest lake district was among the most acidified European ecosystems (Veselý 1987, 1988, 1996, Schaumburg 2000). The original research focused on the development of lake water acidification (and/or recovery, later) (Fott et al. 1987, Veselý et al. 1998a,b, Vrba et al. 2003a, Norton & Veselý 2004), and the increasing significance of nitrate (NO_3^-) in this process (Veselý & Majer 1992, Veselý et al. 2002a). An important part of these studies was the effect of atmospheric deposition and soil acidification on trace metals in acidified waters (Veselý 1997, Veselý & Majer 1996, Veselý et al. 1985, 2002b). The long-term monitoring provided the first step for the following integrated research of the Bohemian Forest lakes and enabled reconstruction of their acidification history (Majer et al. 2003, Oulehle et al. 2012), as well as disentangling effects of acidification and climate change on aluminium (Al) and silica (Si) export from terrestrial to aquatic ecosystems (Veselý et al. 2003, 2005). Since the late 1990s, scientific interest in the Bohemian Forest lakes has also included biogeochemical processes in their catchments (effects of soils and vegetation on water chemistry), chemistry of atmospheric deposition, hydrology and climate, and provided a solid (and necessary) base for the systematic ecological research of the whole catchment–lake systems (for review, see Kopáček & Vrba, 2006). Our current review summarises up to-now progress of this integrated research of the Bohemian Forest lakes and their catchments based on fourteen projects conducted during the past two decades (Table 1).

Site description

There are eight natural lakes of glacial origin in the Bohemian Forest (Fig. 1). Five of them (Černé, CN; Čertovo, CT; Plešné, PL; Prášilské, PR; and Laka, LA) are in the Czech Republic and three others (Rachelsee, RA; Großer Arbersee, GA; and Kleiner Arbersee, KA) in Germany. Bedrock is formed from metamorphic and crystalline rocks (mica schist, gneiss, granite, and quartzite), sensitive to atmospheric acidification (Veselý 1994, Schaumburg 2000). Thus, all the lakes became acidic in the last century (Fott et al. 1987, Kopáček et al. 2002c) and have a depleted carbonate buffering system or low acid neutralising capacity (ANC) at present (Nedbalová et al. 2006, Vrba et al., in prep.).

Mean monthly air temperatures varied between –12.9 and 17.7°C in the CT catchment at elevation of 1057 m in the 1781–2012 period, with long-term averages between –3.5°C in January and 13.9°C in July (Turek et al. 2014). Annual precipitation in a treeless area averaged ~1300 mm in the CT catchment at elevation of 1180 m from 1992–2012 (Hruška et al. 2000, Kopáček et al. 2013b), and lakes are usually frozen for 4–5 months, from December to

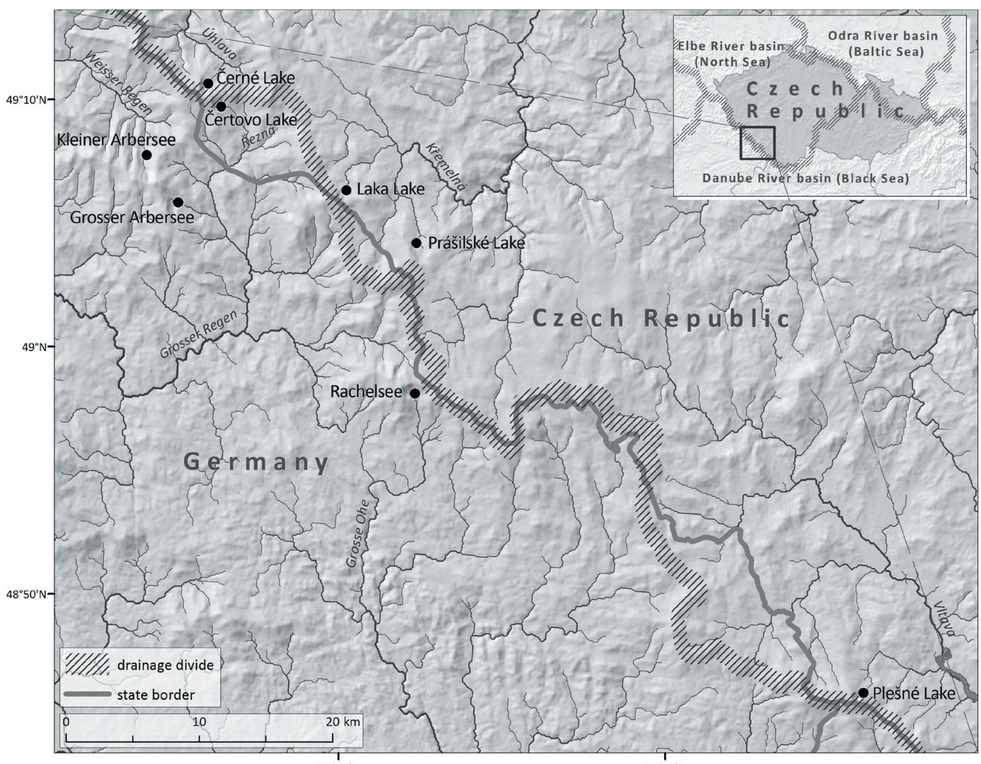

Fig. 1. Map of the LTER site Glacial Lakes showing their location in the Bohemian Forest.

April.

Catchments of the Bohemian Forest lakes are steep (with maximum local reliefs of 235–380 m) and covered with thin, acid lithosol, podzol, and cambisol (Kopáček et al. 2002a,b). Vegetation covers most of the catchment areas and is dominated by 80 to 150 year old Norway spruce forest, with sparse white fir and European beech. The area of both CN and CT catchments has been protected as a nature reserve since 1911. After World War II, access and most kinds of land use were restricted in most of the Czech part of the Bohemian Forest, which was behind the "Iron Curtain", due to border control during the "Cold War" period. The military zone was abolished in 1989 and since that time the area has been again more accessible for scientific research. Most of the lakes belong to the core zone of the Šumava National Park and the Bavarian Forest National Park, declared in 1991 and 1970, respectively. Thus, free access or land use activities (like forestry) remain limited at the lakes, both in the Czech and German parts of the Bohemian Forest. Since the 1990s, a large area of the Bavarian Forest and Šumava National Parks has been affected by bark beetle infestation and Norway spruce stands were severely disturbed in some catchments. The most severe forest dieback occurred in the RA, PL, LA, and PR catchments, while the CT and CN catchments were affected partially (Zimmerman et al. 2000, Kopáček et al. 2009a, 2013c, Oulehle et al. 2013, Vrba et al. 2014).

The Bohemian Forest lakes have become a part of integrated studies on European lake ecosystems within environmental projects of the European Commission: RECOVER:2010 (Predicting recovery in acidified freshwaters by the year 2010; EVK1-CT-1999-00018) and EURO-LIMPACS (Integrated Project to Evaluate the Impacts of Global Change on European Freshwater Ecosystems; GOCE-CT-2003-505540). In addition, several smaller national projects have focused on different aspects of biogeochemistry in the Bohemian Forest catchment–lake systems (Table 1).

During the last two decades, the Bohemian Forest lakes have also been established as one site in the International Long-Term-Ecological-Research (ILTER; e.g. Heurich et al. 2010) network and included in the International Cooperative Programme on Assessment and Monitoring of Acidification of Rivers and Lakes (ICP Waters).

Present research activities

Fourteen recent projects have studied responses of mountain forest and aquatic ecosystems to various environmental drivers during the last two decades (Table 1). The projects cover the integrated catchment–lake approach, especially in the CT and PL catchments, and long-term limnological research of all eight lakes to study key processes and responses of different systems to the decreasing atmospheric pollution and the increasing air temperature. Besides regular monitoring of atmospheric deposition, we have studied water chemistry of the lakes and their tributaries, ongoing chemical and biological recovery of both aquatic and forest ecosystems from acid stress, including soil chemistry, microbial activity, vegetation, and forest disturbances in the lake catchments. Detailed methodologies used in respective projects are described in publications cited below or in Table 1.

Water chemistry, acidification and recovery of the lakes

The Bohemian Forest was exposed to heavy atmospheric pollution during the last century due to high central European emissions of S and N compounds from anthropogenic sources (Kopáček & Veselý 2005, Kopáček & Posch 2011). Since the late 1980s, central European emissions of SO_2, NO_x, and NH_3 have declined ~90%, ~55%, and ~40%, respectively (Kopáček & Hruška 2010, Kopáček et al. 2011b). Deposition of S and N compounds in the

Table 1. Chronological overview of recent projects on the LTER site Glacial Lakes.

Project title (number)	Duration	Coordinator	Institutions [a]	Ref. [b]
Biodiversity of microbial loop, carbon flow and nutrient cycling in acidified lakes in the Šumava Mountains: pathways and controlling mechanisms (CSF 206/97/0072)	1997–1999	Jaroslav Vrba	BC-IHB, CUNI, CGS	1
Biogeochemical cycles of nutrients in mountain catchment–lake ecosystems: Anthropogenic impacts and possibilities of recovery (CSF 206/00/0063)	2000–2002	Jiří Kopáček	BC-IHB, USB, CGS	2
Nutrient cycling in the nitrogen-saturated mountain forest ecosystem: History, present, and future of water, soil, and Norway spruce forest status (CSF 206/03/1583)	2003–2005	Jiří Kopáček	BC-IHB, USB, CGS, CULS	3
Reproduction biology and autecology of the quillworts *Isoëtes echinospora* and *I. lacustris* in Bohemian Forest lakes and in *ex-situ* cultures (CSF206/04/0967)	2004–2006	Štěpán Husák	IBOT	4
EUROLIMPACS (Integrated project to evaluate the impacts of global change on European freshwater ecosystems) (EC GOCE-CT-2003-505540)	2004–2009	Richard Battarbee (Jiří Kopáček)	36 EU partners (BC-IHB)	5
Photochemical transformation of metal and phosphorus species in natural waters (CSF 206/06/0410)	2006–2008	Jiří Kopáček	BC-IHB, USB, CGS	6
Critical factors of reproduction and recovery of the quillwort *Isoëtes lacustris* and *I. echinospora* populations in strongly acidified lakes (KJB 600050704)	2007–2009	Martina Čtvrtlíková	BC-IHB, IBOT	7
Constraints and limits of biological recovery from acid stress: What is the future of headwater ecosystems in the Bohemian Forest? (CSF 206/07/1200)	2007–2011	Jaroslav Vrba	BC-IHB, USB, CUNI, CULS	8
The assessment of impact of the Gothenburg protocol on acidified and eutrophied soils and waters (CZ 0051)	2007–2011	Jakub Hruška	CGS, BC-IHB, NIVA	9
What are the main mechanisms affecting N flow through soil N pools in N saturated mountain soils? (KJB600960907)	2009–2011	Jiří Kaňa	BC-IHB, USB	10
The integrated impact of climate change, air quality, and forest management on water ecosystem in headwater catchments (CSF 526/09/0567)	2009–2013	Evžen Stuchlík	CUNI, BC-IHB	11
Arbuscular mycorrhizal fungi and dark septate endophytes colonising the roots of submerged aquatic macrophytes, *Isoëtes lacustris* and *I. echinospora* (CSF P504/10/0781)	2010–2013	Radka Sudová	IBOT	12
Effects of solar radiation on biogeochemical cycling of nutrients and metals in surface waters (CSF P503/12/0781)	2012–2014	Petr Porcal	BC-IHB	13
The effect of natural dieback of mountain spruce forest on microclimate, chemistry, and bio-diversity of terrestrial and aquatic ecosystems (CSF P504/12/1218)	2012–2016	Jiří Kopáček	BC-IHB, USB, CULS	14

[a] **Coordinating institutions**: BC-IHB – Institute of Hydrobiology, Biology Centre CAS, České Budějovice; CGS – Czech Geological Service, Prague; CULS – Czech University of Life Sciences, Prague; CUNI – Faculty of Science, Charles University, Prague; IBOT – Institute of Botany CAS, Třeboň; NIVA- Norwegian Institute for Water Research, Oslo; USB – Faculty of Science, University of South Bohemia, České Budějovice.

[b] **References of relevant publications**:

1 Hejzlar et al. 1998, Kopáček & Hejzlar 1998, Kopáček et al. 1998a,b, 1999, Procházková & Blažka 1999, Veselý 1998, Veselý et al. 1998a,b;

2 Bitušík & Kubovčík 2000, Borovec 2000, Hruška et al. 2000, Kopáček et al. 2000a–c, 2001a–e, 2002a–c, 2003a, Straškrabová et al. 2000, Veselý 2000a,b, Vrba et al. 2000, 2003a,b, Bittl et al. 2001, Evans et al. 2001, Prechtel et al. 2001, Majer et al. 2003, Veselý et al. 2003;

3 Kettle et al. 2003, Kopáček et al. 2003b, 2004, 2005a,b, Vacek & Podrázský 2003, Vacek et al. 2003a,b, Podrázský et al. 2004, Porcal et al. 2004, Šantrůčková et al. 2004, Kaňa & Kopáček 2005, 2006, Kopáček & Veselý 2005, Svoboda & Podrázský 2005, Veselý et al. 2005;

4 Čtvrtlíková et al. 2009;

5 Bitušík & Svitok 2006, Jankovská 2006, Kohout & Fott 2006, Kopáček & Vrba 2006, Kopáček et al. 2006b,c, Lukavský 2006, Nedbalová et al. 2006, Nedoma & Nedbalová 2006, Pražáková et al. 2006, Svoboda et al. 2006a–c, Šantrůčková et al. 2006, Tátosová et al. 2006, Vrba et al. 2006, Štefková 2008;

6 Klementová et al. 2009, Kopáček et al. 2006a, 2007, 2008, Porcal et al. 2009, 2010;

7 Čtvrtlíková 2011, Čtvrtlíková et al. 2012, 2014;

8 Šantrůčková et al. 2007, Píšová et al. 2008, Kopáček et al. 2009a,b, 2011a, Matějka 2009, Matějka & Starý 2009, Bárta et al. 2010, Novotná et al. 2010, Svobodová et al. 2012;

9 Šantrůčková et al. 2009, Kopáček & Hruška 2010, Kopáček et al. 2010, Kopáček & Posch 2011, Oulehle et al. 2012, 2013;

10 Tahovská et al. 2010, 2013, Kaňa et al. 2011;

11 Kopáček et al. 2011b, 2012, Norton et al. 2014;

12 Sudová et al. 2011, Kohout et al. 2012, 2014;

13 Porcal et al. 2014;

14 Soldán et al. 2012, Kaňa et al. 2013, 2014, Kopáček et al. 2013a–e, 2014a,b, 2015, Farská et al. 2014a,b, Turek et al. 2014, Vrba et al. 2014, Matějka 2015, Seedre et al. 2015, Stockdale et al. 2014.

Bohemian Forest reflected their emission rates in central Europe (Kopáček et al. 1998a, 2001e). Deposition was relatively stable in the first half of the 20th century, rapidly increased between 1950 and 1980, and reached a maximum in the early 1980s. Estimated maxima were ~165 and ~50 $mmol.m^{-2}.yr^{-1}$ for throughfall and bulk deposition of sulphate (SO_4^{2-}), respectively. Similarly, deposition of NO_3^- and ammonium (NH_4^+) reached their respective maxima of ~100 and ~60 $mmol.m^{-2}.yr^{-1}$ (for throughfall) in the 1980s. During the 1990s, acid deposition decreased substantially, and its current level is similar to the late 19th century for SO_4^{2-} and NH_4^+, and to the middle 1960s for NO_3^- (Kopáček et al. 2001e, 2009b). These changes in acidic deposition have led to a more significant recovery in the Bohemian Forest freshwaters compared to other European lake districts (Evans et al. 2001).

Lake water acidification peaked in the middle 1980s and has been reversing since that time. From the 1980s to the late 1990s, the average (± standard deviation) SO_4^{2-} and NO_3^- concentrations in the eight Bohemian Forest lakes decreased by 19±7 and 15±11 $\mu mol.l^{-1}$, respectively (Kopáček et al. 2002c). The Bohemian Forest was the first lake district exhibiting a consistent decrease in NO_3^- concentrations (Veselý 1996, Veselý et al. 1998a). The decline in concentration of strong acid anions was compensated for by a decrease in concentrations of aluminium (Al; 7±4 $\mu mol.l^{-1}$), protons (H^+; 6±5 $\mu mol.l^{-1}$), and base cations (9±6 $\mu mol.l^{-1}$) (Kopáček et al. 2002c). The trend in lake water recovery from acidification continues until the present, even though at smaller rates than during the 1990s (Majer et al. 2003). The forest dieback due to bark beetle infestation delayed (and even temporally reversed) recovery of water chemistry in some lakes, particularly in RA, LA, and PL (Kopáček et al. 2013c, Oulehle et al. 2013, Vrba et al. 2014).

The acidification history of the Bohemian Forest lakes is best documented for CN. With an area of 18.4 ha and maximum depth of 40 m, CN is the largest and deepest lake in the Bohemian Forest. The first reliable data on lake water chemistry, e.g., pH of 6.3–7.0 and traces of NO_3^- (<2 $\mu mol.l^{-1}$) come from 1936 (Jírovec & Jírovcová 1937). Despite several historical attempts to determine SO_4^{2-} concentrations in CN, the first reliable data (20–30 $\mu mol.l^{-1}$) come from the early 1960s (Procházková & Blažka 1999). This survey already indicated the first effects of atmospheric acidification on the lake composition, predominantly lowered pH (5.4–6.2) and increased NO_3^- concentrations (30–40 $\mu mol.l^{-1}$) compared to the 1930s. The lake water pH decreased to ~4.5 in the late 1970s and acidification progressed until 1986–1988, when NO_3^- and SO_4^{2-} concentrations reached their maxima of 80–100 and 67–76 $\mu mol.l^{-1}$, respectively (Veselý et al. 1998a). Reversal of lake water chemistry has occurred since the late 1980s due to the reduction in S and N emissions and decreasing acidic deposition. Long-term trends in the CN chemistry have been successfully reconstructed by a dynamic, process-based model MAGIC 7 (Modelling the Acidification of Groundwater in Catchments; Cosby et al. 2001). The model was calibrated for a set of records on lake water composition over the 1984–2001 period, and produced hindcast concentrations that compared well to even older irregular determinations of NO_3^-, SO_4^{2-}, and pH (Majer et al. 2003). Modelled SO_4^{2-} concentrations were predicted to decrease to the levels found at the beginning of the 20th century by 2050 (Fig. 2). Similar steep changes in water chemistry occurred also in PL and CT (Majer et al. 2003).

Rapid changes in lake water chemistry, accompanied with steep trends in pH (Fig. 2G) and concentrations of total and ionic Al forms (Fig. 2F,H) enabled studies on effects of water acidification on in-lake nutrient cycling. In contrast to the well-known nutrient transformations in circum-neutral lakes (e.g., Wetzel, 2001), the acidified Bohemian Forest lakes are rich in Al that can precipitate as colloidal aluminium hydroxide ($Al(OH)_3$) after an increase in water pH. $Al(OH)_3$ has a large surface area and can strongly bind P from the liquid to the particulate phase, immobilise orthophosphate in the water column, and prevent its release from sediments (Kopáček et al. 2000a, 2001d, 2004).

Analyses of the PL sediment, however, showed that Al has affected P chemistry in the Bohemiam Forest lakes since soil formation in the catchment at the beginning of Holocene, i.e., long prior to their atmospheric acidification (Kopáček et al. 2007, 2009a). This Al originates from photochemical cleaving of organic-metal complexes transported to lakes by their tributaries from soils (Kopáček et al. 2005b, 2006a). In addition, photochemical (and bio-

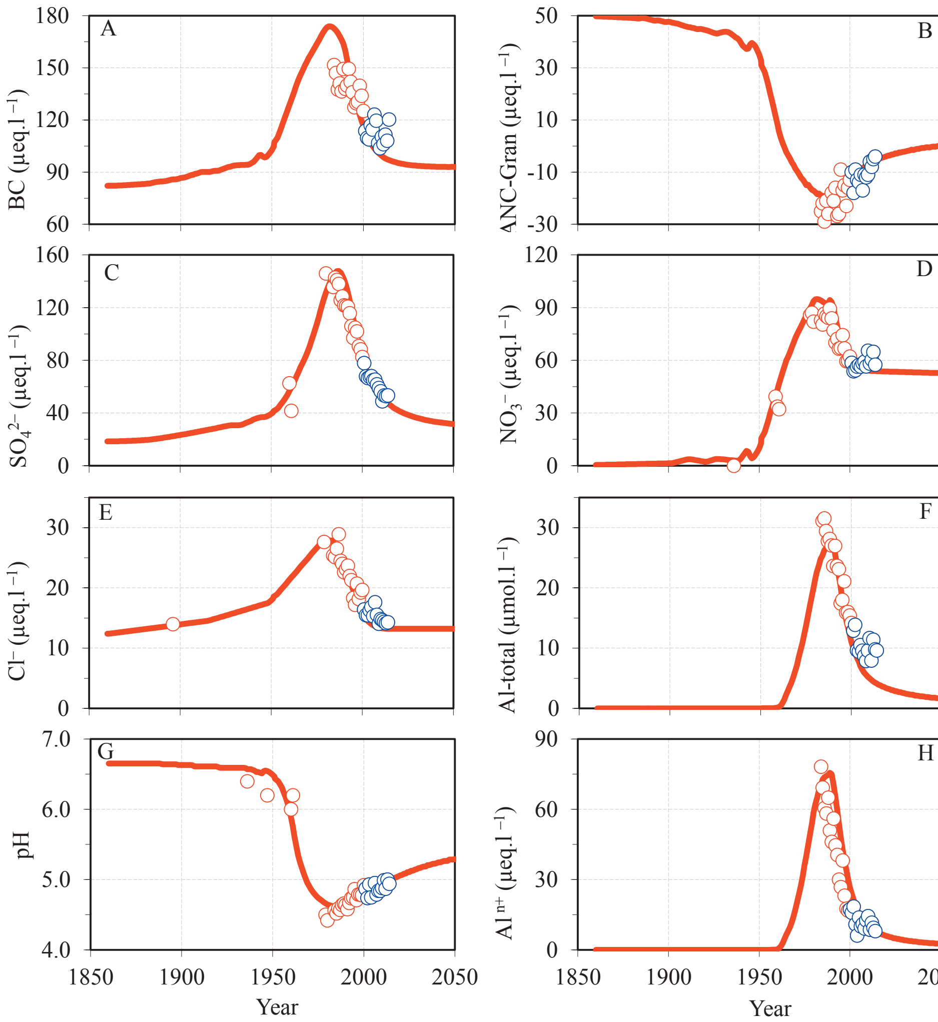

Fig. 2. Measured (open circles) and modelled (lines) trends in water chemistry of Černé Lake. The model (MAGIC 7; Cosby et al. 2001) was calibrated on long-term data prior to year 2001 (red circles). The forecast is based on the projected decrease in S and N emission/deposition rate in central Europe according to the Gothenburg Protocol (UNECE 1999). Blue circles represent data measured in 2001–2010, which are in reasonable agreement with those predicted by the model. Data are derived from Majer et al. (2003) and Kopáček (unpubl. data). ANC-Gran, acid neutralising capacity determined by Gran titration; BC, base cations (Ca^{2+}+Mg^{2+}+Na^{+}+K^{+}); Al-total, total aluminium; and Al^{n+}, positively charged ionic Al. Except for pH and Al-total, units are microequivalents (μeq); one equivalent is one mole of charge.

logical) degradation of allochthonous dissolved organic carbon (DOC) in lakes is an important in-lake alkalinity producing mechanism (Kopáček et al. 2003a), the second after NO_3^- assimilation and denitrification (Kopáček et al. 2006b,c). The photochemical studies also showed that the increased bioavailability of recalcitrant DOC after its photo-transformations (Porcal et al. 2004) enables higher bacterial than primary production in some lakes (Nedoma et al. 2003) and that photochemical cleaving of allochthonous dissolved organic N is an important source of NH_4^+ for surface waters (Porcal et al. 2014).

Biological recovery of the lakes

Acidification of the Bohemian Forest lakes caused significant changes in their biodiversity (Fott et al. 1994, Soldán et al. 1999, 2012, Vrba et al. 2003a). The lakes had "simplified" food webs during atmospheric acidification due to the extinction of fish and largely reduced zooplankton (Vrba et al. 1996, 2000, 2003a). Consequently, microbial interactions dominated the pelagic food webs and bacterial filaments formed a significant portion of the plankton biomass. The absence of higher trophic levels in the lakes prevented the biological P recycling typical for non-acidified water bodies (Vrba et al. 2003a,b, 2006, Nedbalová et al. 2006).

The acidification history of CN provides insight to the extent and rapidity of biological changes, reflecting changes in water chemistry, in strongly acidified lakes during the acidification and recovery phases. The first survey of crustacean zooplankton in the lake was performed in 1871 (Frič 1872), and zooplankton status has been monitored more or less regularly till present. The pH decline from >6 to ~4.5 and rapid increase in Al concentrations between the 1930s and middle 1980s (Fig. 2) was accompanied by the disappearance of cladoceran species and fish (Vrba et al. 2003a). While most of the planktonic species apparently died off, one of them (*Ceriodaphnia quadrangula*) survived the period of the highest acidity in the littoral zone, although in very low numbers (Fott et al. 1994). Due to the recent pH increase and Al decrease (Fig. 2), *C. quadrangula* has reached its pre-acidification abundance in the shore zone and has even occurred in the open water since 1997 (Vrba et al. 2003a, Nedbalová et al. 2006). Similar trends could be documented for aquatic insects that have well recovered in CN recently (Soldán et al. 2012). The prognosis for potential fish reintroduction into CN remains, however, poor, because the carbonate buffering system is predicted (by MAGIC; Majer et al. 2003) to be re-established (annual average ANC will reach positive values) only around 2050 (Fig. 2B).

Owing to the historical and long-term data, the Bohemian Forest lakes offer a unique opportunity to assess recovery in different groups of organisms and to analyse both environmental and biological constraints of biological recovery. We studied the response of planktonic (phytoplankton, ciliates, rotifers, and crustaceans) and littoral (Ephemeroptera, Plecoptera, Trichoptera, and Heteroptera: Nepomorpha) assemblages to chemical recovery over a twelve-year period (1999–2011). Despite the rapid improvement in water chemistry of all studied lakes, only four have partly recovered so far. These lakes have low (<200 $\mu g.l^{-1}$) Al concentrations (low-Al lakes: GA, KA, LA, and PR). In contrast the other four lakes still remain strongly acidic and have high (>200 $\mu g.l^{-1}$) Al concentrations (high-Al lakes: CT, CN, PL, and RA) (Vrba et al., in prep.). Multivariate analyses revealed that the Al concentrations dominated in structuring the assemblages of phytoplankton, rotifers, and Nepomorpha and also affected crustaceans through the seston C:P ratio. Both direct (toxicity) and indirect (P availability) effects of Al control biological recovery in the Bohemian Forest lakes (Vrba et al. 2006, in prep.). The actual Al concentrations influence both primary and secondary producers in particular lakes (Vrba et al. 2003b, 2006, 2014, Novotná et al. 2010), and apparently control the timing of biological recovery by forming the bottleneck that lags the recovery of the high-Al lakes. For instance, *C. quadrangula* first appeared in CN in 1997, but in closely adjacent CT a decade later, and in RA in 2009, only after the same threshold of Al concentrations was reached (Vrba et al. 2014, in prep.; cf. Stockdale et al. 2014). The harmful Al effect was also recognised as the critical bottleneck preventing reproduction of quillwort populations – *Isoëtes echinospora* in PL until 2004 (Čtvrtlíková et al. 2009, 2012) and *I. lacustris* in CN till present (Čtvrtlíková et al. 2014).

Although biotic responses (especially in the low-Al lakes) showed important signs of recovery, such as re-appearance of indigenous species, decline in eurytopic acid-tolerant species and colonisation of vagile species, the assemblages of all the lakes still suffer from acid stress. Our results also indicate the increasing role of biotic interactions between colonisers and residents, leading to the reconstruction of aquatic food webs in the low-Al lakes (Vrba et al., in prep.). Fish predation may relax the possible community closure in the low-Al fishless lakes. Since 2010, a population of brook trout (*Salvelinus fontinalis*) has established in KA, spawning near its main inflow (T. Ring – pers. comm.), and the same species recently has been seen in GA (J. Hoch – pers. comm.). Sympatric occurrence of brook trout and brown trout (*Salmo trutta*) has been observed in either lake outflow. Another vital population of brown trout has also been confirmed in the outflow of LA (Matěna et al., in prep.), yet not in the lake. However, any spontaneous fish return into the other lakes is impossible (besides still high water acidity) due also to stream barriers at the outflows of CT, CN, PR, RA, and PL.

Soil chemistry, microbial activity, and vegetation in lake catchments

Physical and biogeochemical soil parameters have been studied in detail since 2002 mainly in the CT and PL catchments differing in bedrock composition (mica-schist and granit, respectively) (Kopáček et al. 2002a,b, Kaňa et al. 2014). The soils are acidic, with pH_{CaCl2} values of 3.1–4.3, 2.5–3.3, and 3.2–4.5 in the litter (O), uppermost organic-rich (A), and all deeper mineral horizons, respectively. The current base saturation of soils (9–15%) is in general significantly lowered compared to the modelled pre-industrial values (12–27% in 1860; Majer et al. 2003). Soils contain 1.6–2.8 $mol.m^{-2}$ S (500–900 $kg.ha^{-1}$), which is mostly organically bound, and concentrations of adsorbed SO_4^{2-} are relatively low (on average 3.4% of the total S pool; Kaňa & Kopáček 2005). From 55% to 80% of the current S pools was accumulated between 1930 and 2000 (Kopáček et al. 2001e). At the current S leaching from soils, a new steady state condition between S input and export will be established within the next ~20–40 years (Kopáček et al. 2001e, Majer et al. 2003).

Despite strong acidification and N saturation of the Bohemian Forest soils, their biochemical and microbial activity is large and still maintain relatively high N retention capacity apart from persisting NO_3^- leaching (Oulehle et al. 2013). Most active upper soil horizons (O+A) comprise a majority of total soil N (~70%), of which N in microbial biomass represents ~1–3% (Šantrůčková et al. 2009, Kaňa et al. 2014). Kaňa et al. (2014) show that net N ammonification rates are very variable from negligible values to almost 0.5 $mmol.kg^{-1}.d^{-1}$ of NH_4^+. Net nitrification rate is 0.18 $mmol.kg^{-1}.d^{-1}$ of NO_3^- in O horizon on average (Kaňa et al. 2014). The study on the relative importance of the main soil N pools shows that microbial N pool is up to five times larger than mineral N (NH_4^++NO_3^-) pools in the PL and CT catchments and that N flux, either net or gross, through microbial N pool greatly exceeds total mineral N fluxes (Šantrůčková et al. 2009, Tahovská et al. 2013). Averaged for both catchments, daily microbial N immobilization fluxes in O soil horizon are estimated to be 124, 50, and 24 $mmol.kg^{-1}$ of soil for glycine-N, NH_4-N, and NO_3-N, respectively, while gross ammonification is 25 $mmol.kg^{-1}.d^{-1}$ and gross nitrification only 2.6 $mmol.kg^{-1}.d^{-1}$ (Tahovská et al. 2013). It is highly probable that any disturbance of the large microbial N pool can lead to an increased risk of N leaching from these soils. Our studies further show that tight relation between microbial N immobilization and C availability is a mechanism controlling NO_3^- leaching in the N saturated PL and CT soils (Tahovská et al. 2013, Kaňa et al. 2015).

Systematic differences between the PL and CT catchments have been found for soil P pools and mobility. While granitic PL catchment has been losing P in the long-term, the CT catchment situated on mica-schist accumulates P in soils permanently (Kopáček et al. 2011a). This difference can be explained by: (i) higher ability of granite to release P under acidic conditions to the PL soils and by higher sorption capacity related to higher Al and Fe concentrations in the CT soils (Kaňa & Kopáček 2006); and (ii) higher microbially mediated P flux in the PL soils. Microbial activity is certainly important in the P cycling in organic soils in the both catchments (Šantrůčková et al. 2004). P mobility measured *in situ* is much higher in the PL than in the CT soils (Tahovská et al., in prep.), which is in accordance with the observed highest terrestrial export of P and the highest trophic status of PL among the Bohemian Forest lakes (Vrba et al. 2000).

Studies on forest biochemistry extended our knowledge of element pools in the terrestrial part of the catchment–lake ecosystems, evaluating the standing biomass and the associated nutrients in the tree and understorey vegetation biomass (Svoboda et al. 2006a–c, Seedre et al. 2015). Examining the chemistry of the tree rings and their ^{13}C isotopic signal, Šantrůčková et al. (2007) and Píšová et al. (2008) showed a negative effect of atmospheric pollution on the tree physiology. The spruce trees were adversely affected by soil acidification, declined base cation availability, and increased Al toxicity in soil solutions, and trees most probably suffered also from insufficient intrinsic water use efficiency from the 1950s–1980s. Šantrůčková et al. (2006) presented new data on the decomposition rate and nutrient release from the plant litter of Norway spruce forests in the PL and CT catchments. They highlight the role of understorey vegetation in mineral N cycling and show that litters with the C:N ratio <32 are more susceptible to NO_3^- leaching due to the N excess, which exceeds microbial N demand and remains available for nitrifiers. Moreover, they show that decomposition rate of the spruce litter is lower than that of tissue of understorey vegetation due to its higher lignin content and low nutrient (P and N) availability (Šantrůčková et al. 2006).

Litter fall has been studied in the PL and CT catchments (Kopáček et al. 2010, 2015). Litter (and also foliage) in the CT catchment has lower Ca concentrations and Ca:Al ratios, and higher N concentrations and N:Mg ratios, than in the PL catchment. These characteristics further progress with elevation in both catchments, corresponding to higher acid and N deposition at higher elevation. As a result, concentrations of N, Al, and Fe are higher and concentrations of Ca and Mg, as well as Ca:Al and Mg:Al ratios are lower in most litter categories at high elevation (~1300 m) than at low elevation (~1100 m) plots (Kopáček et al. 2010).

Effect of forest dieback on water and soil chemistry in the lake catchments

After the bark beetle infestation of the PL forest in 2004–2006, the litter fall increased from 5.4 to 42 $t.ha^{-1}.yr^{-1}$ and remained relatively high (5.0 $t.ha^{-1}.yr^{-1}$) until 2013 even though >52% of trees were already broken. The chemical composition of most spruce litter categories changed after infestation, with the most pronounced trends in C (decrease) and Ca (increase) concentrations. Moreover, Mg, K, and P concentrations increased in the PL litter compared to the CT litter due to an increasing proportion of litter from rowan, replacing the dead spruce forest (Kopáček et al. 2015). These changes seriously affected water and soil composition in the disturbed PL catchment.

Prior to bark beetle infestation , the average throughfall fluxes (TF) of Na^+, H^+, SO_4^{2-},

NO_3^-, Cl^-, and total P (TP), were on average 1.5–2.1-fold higher than their precipitation fluxes (PF) in the PL catchment. Higher TF:PF ratios (2.1–9.8) were observed for Mn, K^+, Mg^{2+}, Ca^{2+}, and organic C, N and P forms, while lower ratios (0.6–1.3) occurred for dissolved reactive P and NH_4^+. After the forest infestation, throughfall deposition of ions and nutrients started to decrease in the PL compared to the CT catchment. The greatest and most rapid changes occurred for K^+, DOC, Mg^{2+}, and Ca^{2+}. Their fluxes rapidly decreased to values similar to precipitation fluxes within 6–8 years after the infestations. Slower changes occurred in throughfall fluxes of SO_4^{2-}, NO_3^-, and Cl^-, and negligible changes so far occurred in the throughfall fluxes of NH_4^+ (Kopáček et al. 2013b). The major reason for differing response of throughfall deposition of individual elements to forest dieback (and reduced surface area of canopies) was different contribution of canopy leaching (export from living and decaying canopy tissue) and microbial transformations to the elemental throughfall fluxes

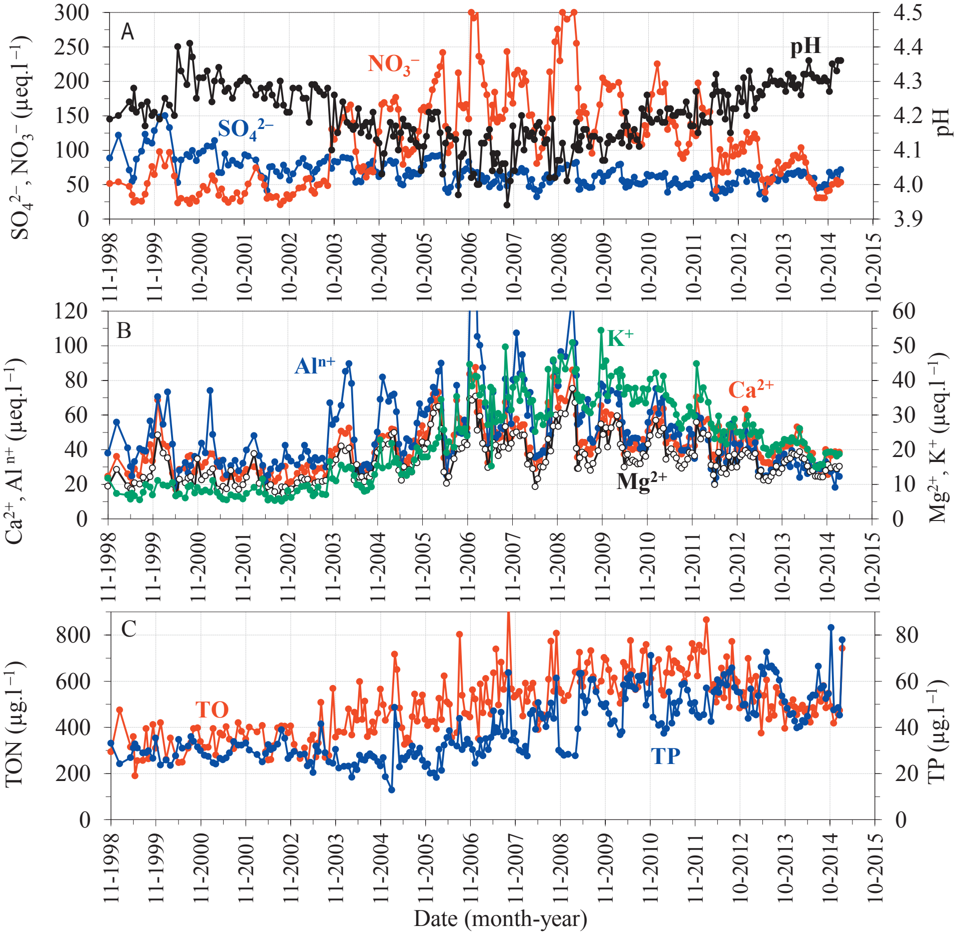

Fig. 3. Time series of pH and concentrations of SO_4^{2-}, NO_3^-, Ca^{2+}, Mg^{2+}, K^+, ionic aluminium (Al^{n+}), total organic nitrogen (TON) and total phosphorus (TP) in the major surface inlet to Plešné Lake. Bark beetle outbreak occurred in the catchment in autumn 2004.

(Kopáček et al. 2009b).

Important changes in water chemistry, associated with bark beetle outbreak in the Bohemian Forest, occurred in all lakes and streams with affected catchments (Kopáček et al. 2013c, Oulehle et al. 2013, Vrba et al. 2014). Prior to the forest damage, water chemistry in lakes and streams exhibited trends typical for areas recovering from strong atmospheric acidification, such as decreasing concentrations of strong acid anions, base cations, Al forms, and protons (increasing pH), similar to the 1989–2006 trends in Fig. 2. After the forest dieback, NO_3^- leaching increased. Nitrate became the dominant anion and its leaching was accompanied by elevated terrestrial export of ionic Al, base cations (especially K^+, Mg^{2+}, and Ca^{2+}), protons (decrease in pH values), total organic N (TON) and TP (Fig. 3). Concentrations of NO_3^- and base cations started to decline ~6 years after the forest dieback, but the elevated leaching of TON and TP continued until the end of this study (Fig. 3). Even in catchments with only relatively small proportion of damaged forests (like CN), the elevated leaching of NO_3^-, base cations, and Al occurred (Oulehle et al. 2013) and levelled off compared to the modelled forecasts of water chemistry based on anticipated trends in acidic deposition (Fig. 2). Our results show that changes in ionic composition of surface waters, following the natural forest dieback, have only relatively short duration within about one decade (Fig. 3A,B). In contrast, it is difficult to predict (on the basis of present data), the effect of forest disturbances on TP and TON losses from the affected catchments (Fig. 3C).

Kaňa et al. (2013) aimed to fill the gap in understanding how the chemistry of forest floor changes following natural forest dieback, when elevated litter decomposition occurs. They integrated the results of a three-year monitoring in six-week sampling intervals. The forest dieback significantly increased concentrations of water extractable NH_4^+, organic N, and P forms. Decomposition of litter in the infested PL catchment elevated concentrations of soil base cations. Base saturation of the PL soils increased from 40 to 70% and from 30 to 45% in the O and A horizons, respectively, as a response to elevated literfall (and reduced tree uptake) after forest bark beetle attack (Kaňa et al. 2013). This increase was based mainly on elevated concentrations of exchangeable Ca^{2+}. Nevertheless, it is most probably that this change only represents a temporary recovery, because these base cations will be used again later by new trees.

Long-term experiments with cellulose decomposition in forest floor in the PL and CT Norway spruce stands showed that cellulose decomposition rates increased after the bark beetle outbreaks and forest dieback in the PL catchment (Kopáček et al. 2015).

Ceased N immobilization by dead trees was identified as the primary cause of elevated N leaching in the PL catchment after forest dieback (Tahovská et al. 2010). However, observed excess of mineral N release to soil water was undoubtedly related also to the soil microbial activity, resulting from a decomposition of elevated litter fall to the forest floor, and indicated by a rapid increase in net ammonification, concentrations of water soluble NH_4^+ and organic C and N, as well as C and N concentrations in microbial biomass. Net nitrification rate and concentrations of NO_3^-, both extractable and measured *in situ*, increased after a delay of 3 years indicating restricted activity of autotrophs (Kaňa et al. 2015).

The elevated production of base cations from decaying litter resulted in decreasing Al concentrations in sorption complex of the PL soils after bark beetle outbreak (Kaňa et al. 2013). The released ionic Al species were immediately complexed with DOC in the soil solutions. Such DOC–Al complexes are not toxic for biota and do not negatively affect roots and organisms in soil, but, being mobile, they can influence recipients. In surface waters, the DOC–Al complexes are cleaved to a large extent by photochemical reactions (Kopáček et al. 2005b). The subsequent hydrolysis of the photochemically liberated Al in the water produces Al hydroxides with a strong ability to bind phosphate. Their increased concentration may thus reduce phosphate mobility and also prevent its release from sediments. This process decreases phosphate bioavailability and affects the primary production and cycling of organic C in lakes (Kopáček et al. 2000a, 2005a, Vrba et al. 2006). This example from the Bohemian Forest catchments nicely shows that element cycles in the catchment–soil–lake systems are not isolated, but closely associated.

Future perspectives

The 14 scientific projects on the Bohemian Forest catchment–lake systems during the last two decades (Table 1) have answered numerous originally postulated questions and hypotheses, focusing on response of different ecosystems compartments to the decreasing atmospheric pollution. The cumulating knowledge and new unexpected ecosystem drivers (e.g., rapidly increasing air temperature and bark beetle-induced forest dieback), however, revealed new gaps in our knowledge and postulated new important questions on ecosystem functioning. Without answering these questions and generalising the results, we will not be able to predict future development of mountain forest and aquatic ecosystems under anticipated changes in environmental conditions, like global warming, spreading of insects and diseases, atmospheric pollution, etc. This review clearly shows the LTER potential of the Bohemian Forest lakes (the sensitive indicators of the changing world) to answer such questions. The integrated research, including all key processes in catchment and aquatic ecosystems, which has been established in the Bohemian Forest during the last two decades, thus provides an excellent (and in many aspects word-unique) basis for the next valuable, whole-ecosystem research.

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