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Nutrient cycling in a strongly acidified mesotrophic lake

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Abstract

In contrast to the well-known nutrient transformations in circumneutral lakes, acidified water bodies may exhibit significant changes in nutrient cycling due to changes in their chemistry and biology. In-lake cycles of carbon (C), nitrogen (N), and phosphorus (P) were evaluated in the strongly acidified Plešné Lake (Central Europe). The lake tributaries had high concentrations of dissolved organic C (DOC), inorganic N, and total phosphorus (TP), resulting in annual averages of 644, 52, and 0.72 μmol L^{-1}, respectively. Because of the absence of fish and largely reduced zooplankton, Plešné Lake has a ''simplified'' food web. The mass balance of nutrients was based on the major external inputs (tributaries and atmospheric deposition), internal sources and transformations (primary and bacterial production, biological decomposition of sedimenting seston and sediments), sedimentation, and outputs. External inputs of total organic C (TOC), total N (TN), and TP into Plešné Lake were 7,244, 864, and 8.6 mmol m^{-2} yr^{-1}, respectively. Net primary production of particulate C (C_{part}) and extracellularly released DOC were 3,205 and 613 mmol m^{-2} yr^{-1}, respectively. Bacterial C_{part} and total inorganic C production were both 1,518 mmol m^{-2} yr^{-1}. Of the total internal and external inputs of TOC, TN, and TP, the in-lake processes removed 4,551 (50% respiration, 40% sedimentation, and 10% photooxidation), 211 (74% sedimentation and 26% denitrification), and 4.6 (100% sedimentation) mmol m^{-2} yr^{-1}, respectively. Compared to circumneutral lakes, nutrient cycling differed as follows: (1) Liberated orthophosphate from sedimenting seston was converted from a liquid to a particulate phase by colloidal aluminum (Al) in the hypolimnion and deposited. Similar abiotic P immobilization with Al removed 1.6 mmol m^{-2} yr^{-1} from the whole-water column, thus reducing by ~20% the pool of potentially bioavailable P and contributing to a severe P limitation of biomass. (2) The cessation of nitrification due to long-term water acidification led to an atypical situation in which the lake became a net source of NH_4^+ (30 mmol m^{-2} yr^{-1}) because dissimilative liberation of NH_4^+ exceeded its assimilation.

Individual nutrient cycles or fluxes have been evaluated many times in numerous water bodies and are relatively well understood (e.g., Kalff 2002). A simple mass-budget study of lakes including only major inputs and outputs of nutrients is usually sufficient for elements such as phosphorus (P) that have a significant sedimentation component to their cycle (Wetzel 2001). In contrast, the net in-lake removal of carbon (C) and nitrogen (N) does not allow a simple differentiation between sedimentation and other in-lake sinks. The organic N pool can be increased by N_2 fixation and inorganic N removed from the water column by assimilation and seston sedimentation, as well as by denitrification in sediments or an anoxic hypolimnion (Kelly et al. 1987; Wetzel 2001). The in-lake mass budget of organic C includes a significant internal source (CO_2 assimilation by primary producers), transformations (respiration and bacterial production), and sinks (photochemical mineralization, coagulation followed by sedimentation, and methane production).

Some of these common processes, however, (e.g., nitrification or P release from sediments) may be more significantly affected in acidified lakes than in those that are circumneutral (Rudd et al. 1998; Kopáček et al. 2000). Severe lake acidification has led to the absence of fish and largely reduced zooplankton, removing these higher trophic levels from internal nutrient cycles, and ''simplifying'' them (Schindler 1988, 1994; Straškrabová et al. 1999). The chemical and biological changes in acidified lakes have thus led to the development of patterns in nutrient cycles that are distinct from those occurring in circumneutral water bodies. Most of the lakes sensitive to acidification are oligotrophic waters with very low natural nutrient concentrations (e.g., Schindler 1994), making the reliable estimation of individual nutrient fluxes methodologically difficult. Plešné Lake (a central European forest lake) represents an exception among atmospherically acidified water bodies, being strongly acidic (pH < 5) for several decades but also rich in nutrients because of the high natural export of P and C from terrestrial sources (Kopáček et al. 2000). This situation provides an opportunity to study the simplified nutrient fluxes in a strongly acidified lake with reasonable resolution, because most nutrient forms are present in concentrations high enough to permit precise and accurate determination.

The aim of this study was (1) to evaluate major fluxes and transformations of C, N, and P forms, including sedimentation, primary and bacterial production, dissimilation, and denitrification in strongly acidified Plešné Lake, and (2) to identify and quantify nutrient fluxes differing from those in circumneutral lakes.

Materials and methods

Description of study sites—Plešné Lake is situated in the Bohemian Forest (Czech–Austrian border, 48°47′N,

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13°52′E; ~150 km south of Prague) at an altitude of 1,090 m above sea level. It is a dimictic lake of glacial origin with an area of 7.5 ha, maximum depth of 18 m, and theoretical water residence time of <1 yr. The lake volume is 6.17×10^5 m^3, of which 39%, 35%, and 26% are in the 0-4-m, 4-9-m, and 9-18-m layers, respectively. The lake was already atmospherically acidified in the early 1960s (pH <5.4), and acidification progressed until the middle 1980s, when pH ranged between 4.4 and 4.7 (Veselý et al. 1998). At present, the lake is in the process of chemical reversal from acidification, with pH approaching ~5, but it still has a depleted carbonate buffering system, and sulphate (SO_4^{2-}) remains the dominant anion (Kopáček et al. 2000). Plešné Lake is fishless, submersed littoral macrophytes are sparse (~0.02 ha), zooplankton are present in low densities (<1% of the total plankton biomass, mainly represented by *Heterocope saliens* and pelagic rotifers), and the phytoplankton community is dominated by acid-tolerant species of green algae, dinoflagellates, and filamentous cyanobacteria (Vrba et al. 2003).

The watershed of the lake (66.6 ha, including the lake) is steep, with a maximum local relief of 288 m, and covered with a thin lithosol, podzol, and spodo-dystric cambisol. The bedrock is made up of granites. The forest covering most of the watershed averages 160 yr of age and is dominated (99%) by Norway spruce. The forest soils of Plešné watershed are important sources of P and organic C for surface tributaries and the lake.

Water sampling and analyses—Nutrient input (terrestrial export via tributaries and precipitation—bulk collectors) and output were based on mass balances of water and its chemical constituents within the Plešné watershed–lake ecosystem in the 2001 hydrological year (November 2000 to October 2001). The water balance was based on the atmospheric deposition (precipitation and two throughfall plots differing in elevation), measured outflow from the lake (a gauge-recorder at a weir), and the budget for chloride (Cl^-), assuming that Cl^- behaved conservatively with no net retention or production within the whole ecosystem. The element fluxes were obtained by linking volume or discharge data with the corresponding concentration data by the method of period-weighted mean (Likens et al. 1977).

Atmospheric deposition, tributaries, and outlet were sampled in 2- to 4-week intervals. The water column profile (0.5, 4, 9, 14, and 17 m) was sampled monthly at the deepest point of the lake. Temperature and dissolved oxygen concentrations were measured with the DataSonde 4 (Hydrolab) at 1-m intervals. The annual change in the storage of elements in the lake was calculated using the lake volume and water column composition (five depths along the vertical profile) at the end and beginning of the study.

In the field, samples for chemical analysis were prefiltered through a 200-μm polyamide sieve, except for samples for total inorganic C (TIC) determination (no filtration). A 40-μm sieve was used for tributaries to remove coarse particles resuspended from the stream bed by the sampler. In the laboratory, samples were filtered with either membrane filters (pore size of 0.45 μm) for the determination of ions or with glass-fiber filters (pore size of 0.4 μm) for other analyses, except for samples for pH, acid-neutralizing capacity (ANC, determined by Gran titration), and total concentrations of aluminum (Al), P, and organic N, which were not filtered beyond the field prefilter. TIC, dissolved, and particulate organic C (DOC and C_{part}) were analyzed with a TOC 5000A analyzer (Shimadzu) for unfiltered samples, the filtrate, and by combustion of the glass-fiber filter with the retained particulate organic matter, respectively. Dissolved reactive P (DRP) was determined by the molybdate method (Murphy and Riley 1962). Total and dissolved P (TP and DP) were determined by perchloric acid digestion and the molybdate method according to Kopáček and Hejzlar (1993), but samples were fourfold concentrated by evaporation (with perchloric acid at ~100°C prior to digestion) to obtain a detection limit of ~0.02 μmol L^{-1}. Total and dissolved organic N (TON and DON; the difference between the respective Kjeldahl N and NH_4-N) were determined by Kjeldahl digestion according to Procházková (1960), but 75 ml of samples were evaporated to obtain a detection limit of ~2 μmol L^{-1}. Particulate P (P_{part}) and particulate N (N_{part}) were the differences TP–DP and TON–DON, respectively. Concentrations of NH_4^+, NO_3^-, and other ions were determined by ion chromatography (Dionex IC25). Total N (TN) was the sum of NO_3^-, NH_4^+, and TON (NO_2^- was typically <1% of NO_3^- in all types of samples and was neglected). Concentrations of chlorophyll *a* were determined on Whatman GF/C filters after acetone extraction according to Lorenzen (1967); values were not corrected for phaeopigments.

Fractionation of aluminum according to Driscoll (1984) (i.e., total Al [Al_{total}], dissolved Al, and organically bound Al [Al_o]) were analyzed in nonfiltered samples, filtered samples, and cation exchange–treated samples after their filtration, respectively, using the method of Dougan and Wilson (1974). Ionic Al (Al_i) was the difference between dissolved Al and Al_o concentrations. Particulate Al (Al_{part}) was the difference between total and dissolved Al concentrations.

Sedimentation rate and sediments—Sedimenting particulate matter was collected in sediment traps (Plexiglas tubes, 300 mm long and 50 mm in diameter; duplicates) situated in the 9-m depth (chemically the most stable water layer; *see* below) at the deepest point of the lake. The samplers were exposed for 2- and 1-month intervals in winter and ice-free periods, respectively. Suspended material from the traps was homogenized by shaking and analyzed for concentrations of C_{part} and N_{part} (as described for water) and P_{part} and Al_{part} (the differences between the respective P or Al concentrations in the suspension and filtrate, determined by nitric/perchloric acid digestion according to Kopáček et al. [2001]). We assumed that the sediment deposition on the bottom was negligible in the epilimnion and littoral zone as a result of intensive water mixing and sediment resuspension and that all allochthonous and autochthonous particulate material was distributed and stored uniformly under the thermocline (usually below the 4-m depth). The sedimentation rate of elements, given on a lake area basis (R_L; g m^{-2} yr^{-1}), was obtained as $R_L = R_{9m}A_T/A_L$, where R_{9m} (g m^{-2} yr^{-1}) is the measured sedimentation rate in the 9-m depth, and A_T and A_L are the thermocline (5.2 ha) and lake areas, respectively.

Concentrations of C, N, P, and Al in the Plešné sediment were averaged for the surface layers (0–10 cm) of seven sediment cores, sampled from >16-m depths. Element concentrations were determined as described for sedimenting particulate matter in lyophilized samples. The average mass accumulation rate (60 g m^{-2} yr^{-1}, given on a lake area basis) was calculated from the average accumulation rate of fresh sediments (5.3 mm yr^{-1}; Schmidt et al. 1993), water content of the uppermost sediment layer (98.4%), and the thermocline and lake areas as described for sedimentation rate. This accumulation rate was ~2-fold higher than in the other less-productive Bohemian Forest lakes (Veselý et al. 1993, pers. Comm..). Long-term element accumulation in the sediments was the product of concentration and mass accumulation rate.

Primary production—Phytoplankton primary production of C_{part} and extracellular production of DOC (EDOC) were measured monthly by a ^{14}C method (4-h incubation) in the 0.5-m and 4-m depths at the deepest point of the lake, following Straškrabová et al. (1999). The 4-m depth represented the lower part of the epilimnion. The annual in-lake primary production of C_{part} and EDOC were obtained as follows. (1) The experimental rates were recalculated to average daily rates (μmol L^{-1} d^{-1}) using an average length of ‘‘photosynthetically active’’ daylight, arbitrarily estimated as the difference between sunset and sunrise, minus 2 h as a correction for less-intensive radiation in the morning and evening. The C_{part} primary production was then corrected for phytoplankton respiration during the night to obtain a net primary production of C_{part}, assuming that respiration during 1 h of the dark equaled 28% of the production during 1 h of the light (Wetzel 2001). (2) Primary production in the 0–2-m and 2–4-m layers during each sampling period was the product of their volumes, the net rates of primary production in the 0.5- and 4-m depths, respectively, and the period length. Total in-lake primary production was the sum for both layers. The length of a sampling period was calculated as the sum of half the interval between one sampling date and the previous one, plus half the interval between the same sampling date and the following one. (3) The annual in-lake primary production of C_{part} or EDOC (mol m^{-2} yr^{-1}) was the sum for all sampling periods divided by lake area.

Bacterial production—Bacterial production of C_{part} was measured by the ^{3}H-thymidine method, as described by Straškrabová et al. (1999), at the same place, depths, and intervals as primary production, but incubation lasted 1 h in summer and 3 h in winter (low temperature). The measured rates of bacterial production were assumed to represent the whole sampling period. Bacterial productions at the 0.5- and 4-m depths were assumed to represent the whole layers 0–3 m and 3 m–bottom, respectively (Nedoma unpubl. data), and the total in-lake bacterial production of C_{part} was the sum for both layers. The annual in-lake bacterial production of C_{part} (mol m^{-2} yr^{-1}) was the sum for all sampling periods divided by lake area. The total DOC decomposition associated with bacterial growth was estimated as a twofold measure of C_{part} bacterial production, because the yields of C_{part} and TIC (CO_2) from the bacterially decomposed organic matter are assumed to be ~50% each (Wetzel 2001).

Table 1. The volume (discharge) weighted mean composition of precipitation, lake input (tributaries), and output (Plešné Lake, 2001 hydrological year). Average pH values were calculated from the average H^+ concentrations. All numbers are μmol L^{-1}, except for pH and acid neutralizing capacity (ANC, determined by Gran titration; μeq L^{-1}).

	Precipitation	Tributaries	Outlet
DOC	77	644	295
C_{part}	40	26	223
NH_4^+	26.2	0.7	5.7
NO_3^-	23.3	51.1	22.1
DON	8.2	20.7	12.9
N_{part}	6.9	0.8	13.8
DRP	0.40	0.59	0.03
DP	0.43	0.69	0.07
P_{part}	0.21	0.03	0.26
Al_i	<0.2	16.3	8.5
Al_{part}	<0.2	0.6	4.7
ANC	−13	−46	−7
pH	4.94	4.43	4.93

Dissimilation of sedimenting seston in the hypolimnion—The hypolimnetic production of P, NH_4^+, and TIC (as CO_2) by the biological decomposition of both sedimenting seston and sediment was estimated using changes in their concentrations below the 9-m depth during periods of lake stratification. In this calculation, the element concentrations in the 9-, 14-, and 17-m depths were assumed to represent the 9–12-m, 12–15-m, and 15 m–bottom layers, respectively. An element's production was the difference between its hypolimnetic amounts at the end and beginning of the stratification period, recalculated proportionally for the whole November–April and May–October periods. The annual hypolimnetic production of elements (mol m^{-2} yr^{-1}) was the sum for both periods divided by lake area.

Results

Nutrient concentrations and sedimentation rates—Nutrient and Al concentrations in tributaries were dominated (>95%) by dissolved forms, whereas C_{part}, N_{part}, P_{part}, and Al_{part} represented a significant or even dominant (in the case of P) fraction in the outlet (Table 1). Tributaries were the principal source of all nutrients but NH_4^+, which mostly originated from atmospheric deposition (Table 2). The total external inputs of total organic C, TN, and TP into Plešné Lake were 7,244, 864, and 8.6 mmol m^{-2} yr^{-1}, respectively. Net removal of dissolved nutrient forms was 88%, 57%, and 44% for DP, NO_3^-, and DOC, respectively, but the lake was a net source of C_{part}, N_{part}, P_{part}, and NH_4^+ (Table 2).

The temperature stratification of Plešné Lake developed characteristically for a dimictic temperate lake, with the exception of an incomplete spring overturn, in which the water layer below 14 m was not completely mixed (Fig. 1).

The chemical composition of the water column was more stable in the winter than in the ice-free period. Major changes in the epilimnion composition occurred during the period of maximum phytoplankton growth from July to October, when chlorophyll *a* and C_{part} concentrations varied between

Table 2. Mass balance of major nutrients in Plešné Lake in the 2001 hydrological year. Total external input includes tributaries and atmospheric deposition on the lake surface. Negative values of net production indicate a new removal. The balance does not include primary and bacterial production. All numbers are mmol m^{-2} yr^{-1}, given on the lake area basis.

	Atmospheric deposition	Tributaries	Change in in-lake storage	Output	Net production
DOC	108	6,805	411	3,471	−3,031
C_{part}	56	275	1.1	2,628	2,298
NH_4^+	37	7	7.1	67	30
NO_3^-	33	540	−12	261	−324
TON	21	227	16	314	82
DON	12	218	12	152	−66
N_{part}	9	9	4	162	148
TP	0.91	7.64	−0.03	3.97	−4.62
DP	0.61	7.28	0.10	0.88	−6.91
P_{part}	0.30	0.36	−0.13	3.09	2.30
Al_{total}	0.2	289	5	199	−85
Al_i	<0.2	172	15	100	−57
Al_o	<0.2	111	11	44	−56
Al_{part}	<0.2	6	−21	55	28

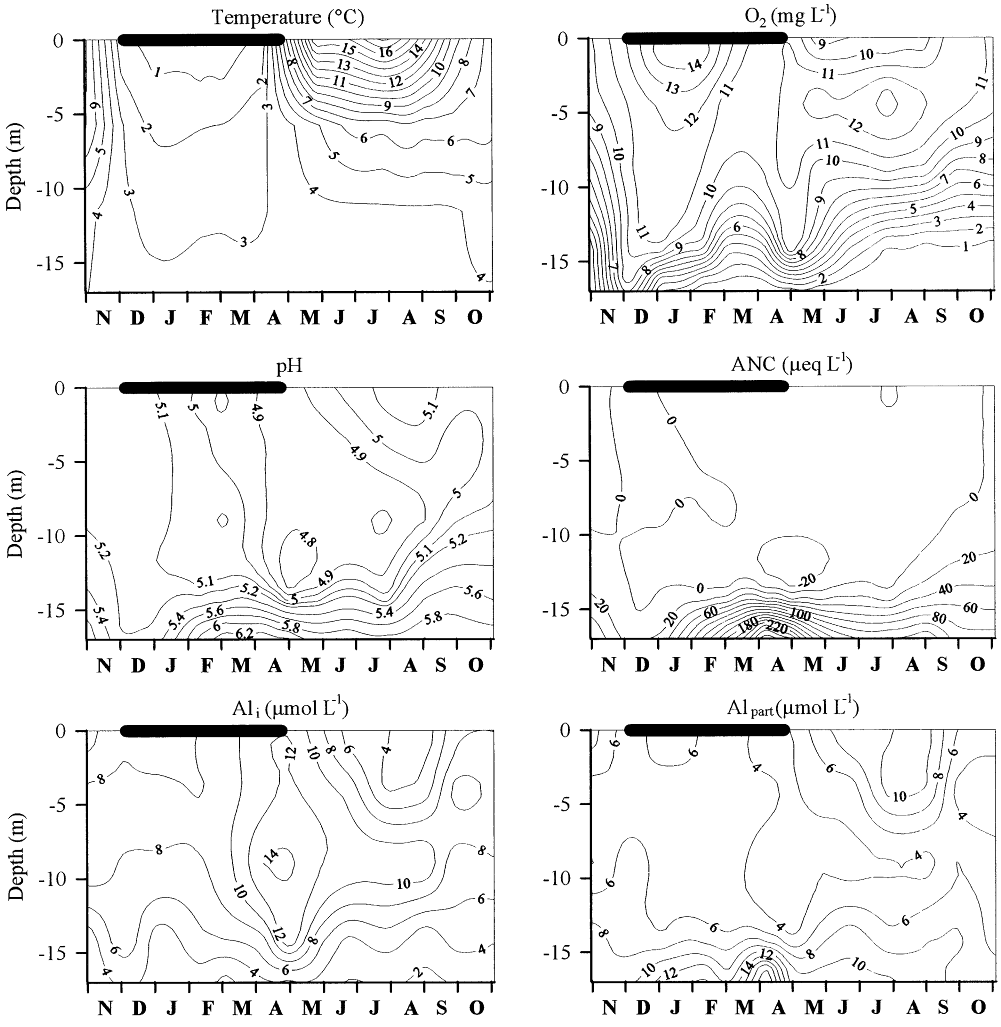


Fig. 1. Depth–time diagrams of temperature, pH, and concentrations of dissolved oxygen (O_2), acid-neutralizing capacity (ANC; Gran titration), and ionic and particulate Al (Al_i, Al_{part}) in Plešné Lake in the 2001 hydrological year. Thick lines represent ice-cover.

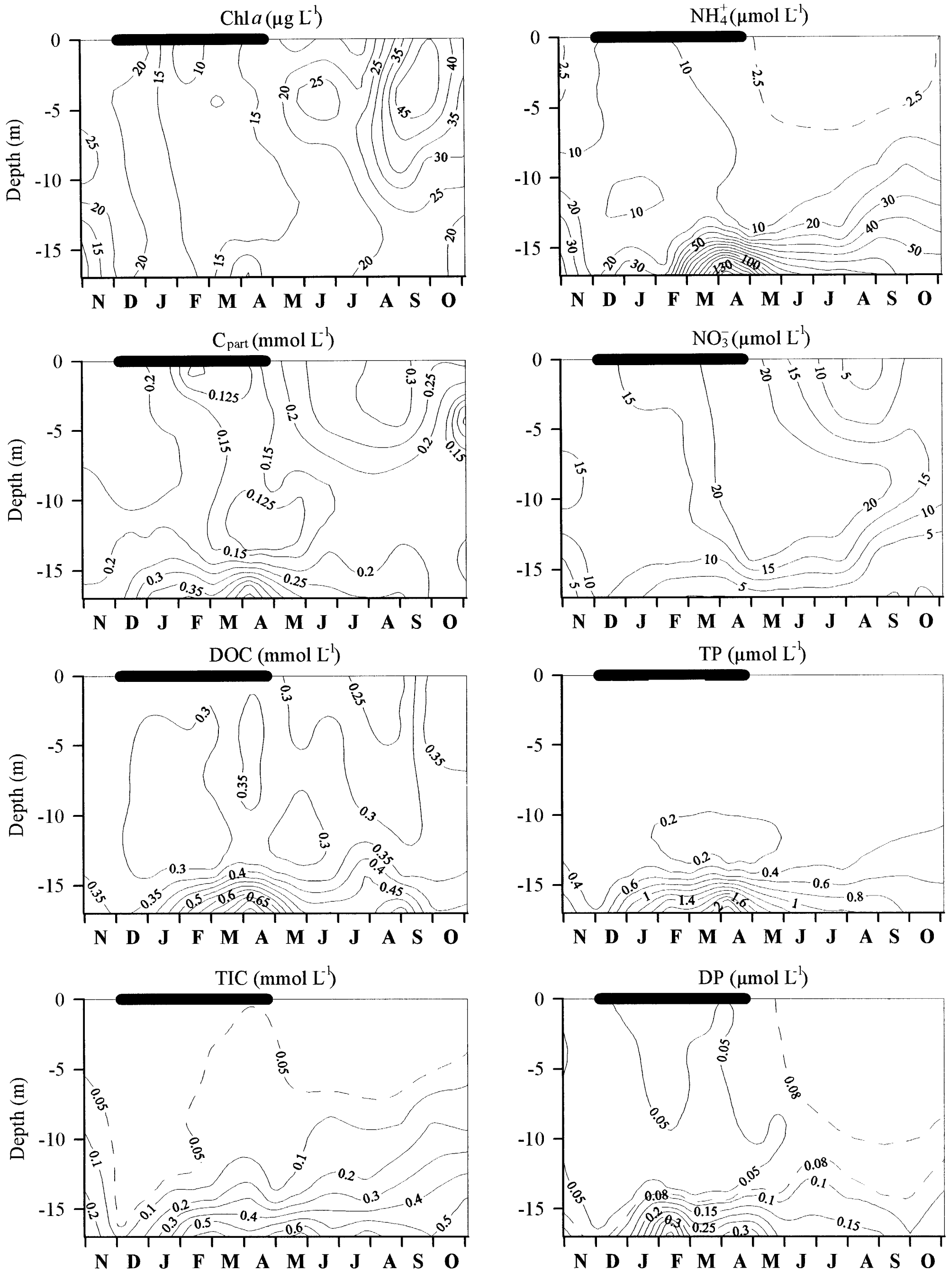


Fig. 2. Depth–time diagrams of chlorophyll *a* (Chl *a*), dissolved organic, particulate and total inorganic carbon (DOC, C_{part}, TIC), NH_4^+, NO_3^-, and total and dissolved phosphorus (TP, DP) concentrations in Plešné Lake in the 2001 hydrological year. Thick lines represent ice-cover.

25 and 49 μg L^{-1} and between 250 and 330 μmol L^{-1}, respectively (Fig. 2). The increased assimilation of nutrients led to a significant reduction in the epilimnetic NH_4^+, NO_3^-, and TIC concentrations (Fig. 2), an increase in pH, and the consequent Al_i hydrolysis and Al_{part} formation (Fig. 1). The annual average (± standard deviation) concentrations of C_{part}, N_{part}, and P_{part} in the Plešné epilimnion were 218 ± 70, 18 ± 6, and 0.26 ± 0.06 μmol L^{-1}, respectively.

Hypolimnetic concentrations of dissolved oxygen were depleted to values <1 mg L^{-1} in the bottom layer during both the winter and summer stratification periods, and also during the incomplete spring overturn. At the low redox potentials, dissimilatory reduction occurred, decreasing concentrations of NO_3^- (Fig. 2) and $SO_4^=$ and increasing concentrations of ferrous ions (Kopáček unpubl. data). The associated alkalinity production led to the hypolimnetic pH and ANC increase and a re-establishment of the carbonate buffering system (positive ANC) below ~14-m depth (Fig.

Table 3. Sedimentation rate of major nutrients and aluminum in Plešné Lake. All numbers are mmol m^{-2} yr^{-1}, given on the lake area basis.

	C_{part}	N_{part}	P_{part}	Al_{part}
Sedimentation rate in 2001*	2,211	201	3.8	62
Storage in sediments in 2001†	1,828	156	4.6	85
Long-term accumulation in sediment‡	1,761	144	5.8	81

* Sedimentation rate measured in 9-m depths using sedimentation traps.

† The C_{part} and N_{part} storage in sediments was the difference between sedimentation rate of C_{part} and N_{part} and dissimilative TIC_{SD} (total inorganic C from seston and sediment dissimilation) and NH_4^+ production in the hypolimnion, respectively. The P_{part} and Al_{part} storage in sediments was set equal to the net in-lake retention of total P and Al (Table 2).

‡ Long-term element accumulation in the sediment was estimated from the average composition of its surface layer (0–10 cm) and average mass accumulation rate.

1). As was the case in the epilimnion, the hypolimnetic concentrations of Al_{part} increased along with the increasing pH gradient as a result of Al_i hydrolysis. The chemically most stable layer, with lowest variations in Al_{part} and NO_3^- concentrations and pH, was between 8 and 12 m (the layer with sediment traps).

Concentrations of TIC, NH_4^+, and TP above the bottom were elevated throughout the year (Fig. 2). They increased rapidly after the autumn overturn, reached a maximum in March and April, decreased slightly during the incomplete spring overturn in May, and then steadily increased until October (Fig. 2). The estimated hypolimnetic production of TIC, NH_4^+, and TP was 1,135, 77, and 1.1 mmol m^{-2} yr^{-1}, respectively (based on changes in their concentration in water below the 9-m depth).

The C, N, P, and Al concentrations averaged 29.6, 2.4, 0.097, and 1.36 mmol g^{-1} of dry weight, respectively, in the surface layer of the Plešné sediment. The long-term average accumulation of these elements in the sediment and their sedimentation rates (measured using sedimentation traps in the 9-m depth) in the 2001 hydrological year are given in Table 3.

Primary and bacterial production—Both primary and bacterial production exhibited significant seasonal variation, with minima in winter, elevated values after ice-melt, and maxima in autumn (Fig. 3). This pattern corresponded well with chlorophyll *a* concentrations in the epilimnion (Fig. 2). Significantly higher net primary and extracellular productions were observed in the 0.5-m depth (Fig. 3A,B), with a higher light intensity (transparency varied between 1.0 and 1.8 m) than in the 4-m depth. More pronounced light attenuation due to the increased C_{part} concentrations (Fig. 2) further reduced primary production in the 4-m depth during autumn. The low primary production in the 4-m depth indicates that neglecting the deeper (>4-m) layers did not seriously affect the estimates of net primary production of C_{part} and EDOC, which accounted for 3,205 and 613 mmol m^{-2} yr^{-1}, respectively (Fig. 3D).

The total bacterial production was 1,518 mmol m^{-2} yr^{-1} (Fig. 3D). The associated in-lake TIC production due to bacterial decomposition of DOC was assumed to be equal to bacterial production. The resulting amount of DOC utilized by bacterial growth was twice that of bacterial production (i.e., 3,036 mmol m^{-2} yr^{-1}). The rate of bacterial production was comparable in both the 0.5- and 4-m depths (Fig. 3C). Nedoma (unpubl. data) observed relatively stable rates of bacterial production in Plešné Lake, even between the 2- and 10-m depths, in a previous year. However, bacterial production in the cold bottom layers could differ. Consequently, the accuracy of the estimated bacterial production could be lower than that for primary production, but could still display an acceptable level of uncertainty for the mass balance, because the lake volume below the 10-m depth represented only ~20% of the total volume.

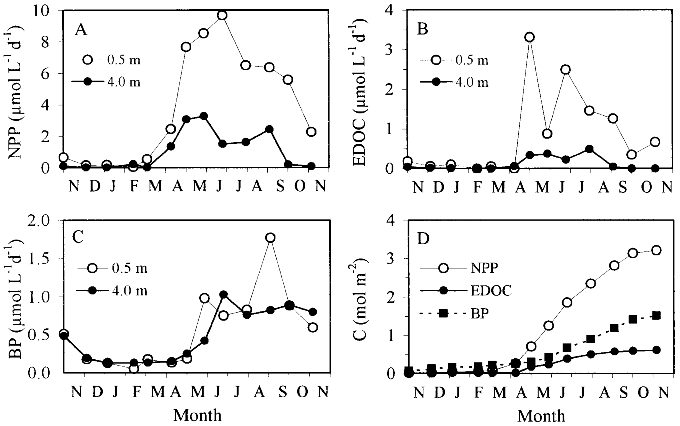


Fig. 3. Primary and bacterial production in Plešné Lake in the 2001 hydrological year. A) Net primary production (NPP) of C_{part} corrected for algal respiration during night. B) Extracellular DOC production (EDOC). C) Bacterial production (BP) of C_{part}. D) Cumulative curves of NPP and EDOC in the epilimnion (0–4 m), and BP in the whole lake.

Assuming similar rates of bacterial production in the water column, we estimated the hypolimnetic production of TIC associated with the bacterial DOC decomposition below 9 m (i.e., below the sediment traps). This TIC flux equaled the bacterial production of C_{part} (376 mmol m^{-2} yr^{-1}) in the 9-m to bottom layer.

Discussion

Dissimilative liberation of nutrients in the hypolimnion—Orthophosphate is the primary P form liberated from the sedimenting organic matter by dissimilatory processes (Wetzel 2001). However, concentrations of DRP were undetectable throughout the water column, because orthophosphate was removed from the liquid phase by colloidal Al and converted to a particulate form (Kopáček et al. 2000). This conversion probably included several processes like orthophosphate adsorption onto Al_{part} (McLaughlin et al. 1981) and coprecipitation of Al-hydroxo-phosphate complexes (Ulrich and Pöthig 2000). The different fate of orthophosphate, as opposed to liberated CO_2 and NH_4^+, which remain dissolved in the water, caused differences between the hypolimnetic and epilimnetic $C_{part}:N_{part}:P_{part}$ ratios (Table 4). Whereas the $C_{part}:N_{part}$ ratio did not significantly change during the seston sedimentation, the $C_{part}:P_{part}$ and $N_{part}:P_{part}$ ratios decreased with depth. The sediment of Plešné Lake was not a

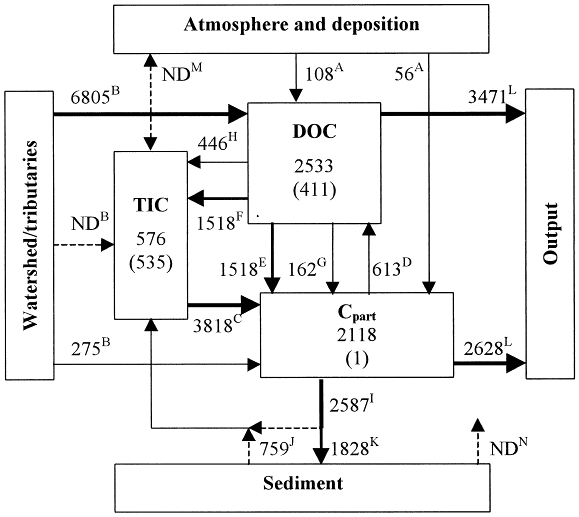
Table 4. The C : N : P molar ratios in tributaries, hypolimnetic and epilimnetic seston, sedimenting material, and sediments in Plešné Lake in the 2001 hydrological year.

	$C_{part} : N_{part}$	$C_{part} : P_{part}$	$N_{part} : P_{part}$
Seston in the epilimnion (0.5 m)*	12.9	822	66
Sedimenting material (9 m)*	11.0	576	52
Seston in the hypolimnion (0.5 m above bottom)*	11.8	342	29
Sediment (0–10 cm)	12.2	306	25
Direct atmospheric deposition*	5.8	187	32
Marine plankton composition (Redfield 1958)	6.6	106	16
Particulate matter of lakes (Hecky et al. 1993)	11.5	306	24
Dissimilative C, N, and P production in the hypolimnion†	$TIC_{SD} : NH_4^+$	TIC_{SD} : TP	NH_4^+ : TP
	9.8	722	74

* Annual average.

† Estimated from the TIC_{SD} (total inorganic C from seston and sediment dissimilation), NH_4^+, and TP production below the 9-m depth.

P source even under anoxic conditions and could not account for the change. The upper sediment layer was enriched with Al oxyhydroxides, which bound orthophosphate liberated from iron (Fe) oxyhydroxides after Fe^{III} reduction to Fe^{II} and prevented P release into the water column (Kopáček et al. 2000). Consequently, the decrease in the hypolimnetic C_{part} : P_{part} and $N_{part} : P_{part}$ ratios originated predominantly from inorganic P_{part}, which was microbially and chemically transformed from the sedimenting seston.



A	Direct atmospheric input.
B	Input by tributaries; TIC input – not determined.
C	Photosynthetic C fixation; the sum of net primary production of C_{part} (3205) and extracellular production of DOC (613).
D	Extracellular production of DOC.
E	Bacterial production of C_{part}.
F	TIC production from bacterial DOC decomposition.
G	C_{part} production by coagulation of DOC.
H	Photochemical mineralization of DOC.
I	Sedimentation of C_{part}; the sum of sedimentation rate (2211) and bacterial production below sediment traps (376).
J	TIC production by dissimilation of sedimenting seston and sediment (TIC_{SD}).
K	Net C_{part} storage in sediments; the difference between the fluxes (I) and (J).
L	Output from the lake by outflow.
M	CO_2 exchange between the lake and atmosphere.
N	Methane production in sediments; probably negligible (<30 mmol m^{-2} yr^{-1}).

Fig. 4. Major fluxes and transformations of carbon forms in Plešné Lake in the 2001 hydrological year: DOC, dissolved organic C; C_{part}, particulate C; TIC, total inorganic C; and ND, not determined. Arrows represent C fluxes (mmol m^{-2} yr^{-1}). Boxes represent pools of C forms (mmol m^{-2}) with annual changes in their storage in the lake (mmol m^{-2} yr^{-1}) given in brackets.

The carbonate buffering system of the water entering the lake was depleted, including that of subsurface tributaries (Kopáček unpubl. data). The hypolimnetic TIC production was thus associated with biochemical processes and not with subsurface external inputs of bicarbonate. The hypolimnetic TIC production (1,135 mmol m^{-2} yr^{-1}) originated not only from dissimilation of sedimenting seston and sediment but also from the bacterial decomposition of DOC. The latter flux was roughly estimated as 376 mmol m^{-2} yr^{-1} (*see* above). The resulting TIC production by the seston and sediment dissimilation (TIC_{SD}) was 759 mmol m^{-2} yr^{-1}.

The molar ratios of nutrients released from seston and sediment in the hypolimnion ($TIC_{SD} : NH_4^+$, TIC_{SD} : TP, and NH_4^+ : TP) were comparable to the annual average $C_{part} : N_{part}$: C_{part} ratios in the epilimnion (Table 4). Such an agreement indicates that the hypolimnetic TIC_{SD}, NH_4^+, and TP productions were reasonably estimated.

The in-lake carbon cycle—The total in-lake flux of DOC was 7,526 mmol m^{-2} yr^{-1}, of which 92% was supplied by external sources (mostly by tributaries) and 8% by internal sources (EDOC) (Fig. 4). The DOC output was 3,471 mmol m^{-2} yr^{-1} and in-lake DOC storage increased by 411 mmol m^{-2} yr^{-1}. The resulting total in-lake retention of DOC was 3,644 mmol m^{-2} yr^{-1}. Including the in-lake DOC production as well, the total in-lake DOC retention was higher than the net DOC retention, based only on the balance of external sources (Table 2).

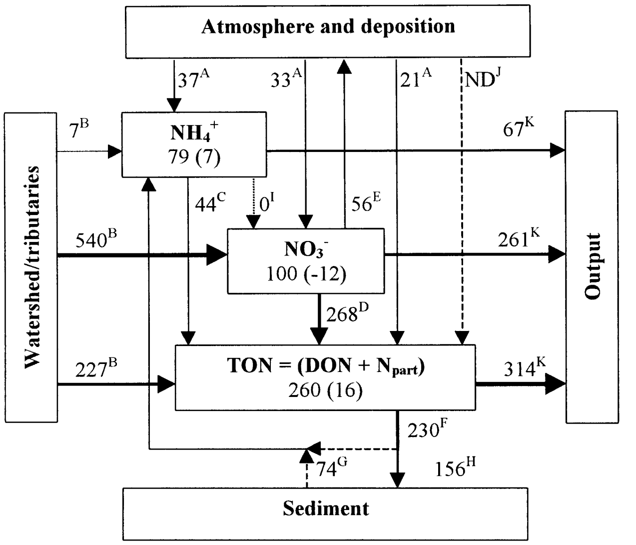
The bacteria decomposed 3,036 mmol m^{-2} yr^{-1} DOC. The difference between total in-lake DOC retention and bacterial DOC decomposition (ΔDOC) was 608 mmol m^{-2} yr^{-1} and represented a part of DOC that was removed from the water column by other processes. Among them, we hypothesize dominant contributions by (1) the coagulation of a large molecular weight (humic) organic matter with Al_{part} (e.g., Driscoll and Postek 1995; Kopáček et al. 2003) and (2) photochemical DOC oxidation to carbon oxides (e.g., Kieber et al. 1989; Bertilsson and Tranvik 2000).

The amount of coagulated DOC (C_{coagul}) was roughly estimated from the balance of C_{part} as follows: The net in-lake production of C_{part} was 2,298 mmol m^{-2} yr^{-1} (Table 2). The C_{part} sedimentation flux in the 9-m depth was 2,211 mmol m^{-2} yr^{-1}, and most of the bacterial C_{part} produced below the 9-m depth (376 mmol m^{-2} yr^{-1}) was also removed from the water column by sedimentation. Thus, the resulting total flux of sedimenting C_{part} was 2,587 mmol m^{-2} yr^{-1}. The sum of net in-lake C_{part} production and total sedimenting C_{part} represented the total in-lake C_{part} production by biotic and abiotic processes (4,885 mmol m^{-2} yr^{-1}). This C_{part} budget was 162 mmol m^{-2} yr^{-1} higher than the sum of in-lake primary and bacterial production of C_{part} (4,723 mmol m^{-2} yr^{-1}). This difference probably originated from the abiotic C_{part} formation by the coagulation of allochthonous humic acids and accounted for ~3% of the external DOC flux. Even though the C_{coagul} flux had a large uncertainty (due to cumulating potential errors in determination of all major C_{part} fluxes), these estimations indicate that the proportion of abiotic C_{part} production was one to two orders of magnitude lower then the biotic C_{part} production in Plešné Lake.

The photochemically mineralized DOC (estimated as ΔDOC–C_{coagul}, i.e., 608–162 = 446 mmol m^{-2} yr^{-1}) represented the amount of DOC that was converted to TIC (carbon oxides) by photooxidation. This amount equaled an ~6% decrease in DOC loading and was threefold higher than results obtained by in situ photochemical experiments with photosynthetically active radiation (PAR) in Plešné Lake in the same hydrological year (Porcal et al. 2004). The experimental results showed that PAR was responsible for the mineralization of 2% of DOC on an annual average. Photochemical mineralization increases rapidly toward the shortest wavelengths (Gao and Zepp 1998). However, short-wavelength radiation is effectively absorbed in the surface-water layer. Thus, in the whole water column, most of the photochemical DOC mineralization is due to ultraviolet-A radiation (39–67%), while PAR contributes somewhat less, with 23–44% (Münster et al. 1999). The calculated total in-lake photochemical mineralization of DOC in Plešné Lake was in the same (3 : 1) ratio to the results of in situ photochemical experiments with PAR (Porcal et al. 2004) and, consequently, seemed to realistically represent this DOC flux.

Of the total sedimenting C_{part}, 759 mmol m^{-2} yr^{-1} was liberated as TIC by microbial decomposition. The resulting amount of C_{part} stored in the sediments was 1,828 mmol m^{-2} yr^{-1}. This C flux was comparable to the long-term average accumulation of C in the Plešné Lake sediments (1,761 mmol m^{-2} yr^{-1}). Such an agreement indicates that major organic C fluxes were estimated with reasonable accuracy.

On an annual basis, the in-lake processes removed 4.55 mol m^{-2} yr^{-1} of the total organic C supplied by both external and internal sources (11.1 mol m^{-2} yr^{-1}). This removal was dominated by CO_2 production from bacterial respiration of both DOC (33%) and seston (17%) and from DOC photooxidation (10%), whereas the C_{part} storage in sediments contributed 40%.



A Direct atmospheric input.
B Input by tributaries.
C NH_4^+ assimilation by biomass.
D NO_3^- assimilation by biomass.
E NO_3^- denitrification in the hypolimnion and sediments.
F Sedimentation of N_{part}; the sum of sedimentation rate (201) and bacterial production below sediment traps (29).
G NH_4^+ production by dissimilation of sedimenting seston and sediment.
H Net N_{part} storage in sediments; the difference between the fluxes (F) and (G).
I Nitrification of NH_4^+ (was absent).
J Nitrogen fixation was not estimated but was neglected.
K Output from the lake by outflow.

Fig. 5. Major fluxes and transformations of nitrogen forms (NH_4^+; NO_3^-; TON, total organic N; DON, dissolved organic N; and N_{part}, particulate N) in Plešné Lake in the 2001 hydrological year. Arrows represent N fluxes (mmol m^{-2} yr^{-1}). Boxes represent pools of N forms (mmol m^{-2}) with annual changes in their storage in the lake (mmol m^{-2} yr^{-1}) given in brackets.

The in-lake nitrogen cycle—On an annual basis, Plešné Lake was a net sink of NO_3^- and a net source of TON and NH_4^+ (Table 2). The net in-lake removal of TN was 211 mmol m^{-2} yr^{-1}. The major fluxes and in-lake transformations of N forms are summarized in Fig. 5 and were estimated as follows.

(1) TON: The total in-lake TON production (312 mmol m^{-2} yr^{-1}) was estimated, similar to C_{part}, as the sum of the following three fluxes: (i) net in-lake TON production (82 mmol m^{-2} yr^{-1}; Table 2), (ii) the N_{part} sedimentation rate in the 9-m depth (201 mmol m^{-2} yr^{-1}; Table 4), and (iii) N_{part} production below the 9-m depth (29 mmol m^{-2} yr^{-1}). The latter flux was calculated from the C_{part} production below the 9-m depth and the average sestonic $C_{part} : N_{part}$ ratio (Table 4). The total in-lake TON production based on the N balance was comparable (~15% lower) with another independent estimate of N assimilation, based on the total primary and bacterial C_{part} production (4,723 mmol m^{-2} yr^{-1}). Considering the average epilimnetic $C_{part} : N_{part}$ ratio (Table 4) for all biotic C_{part} production, the associated N assimilation by biomass was 366 mmol m^{-2} yr^{-1}.

The sum of the N_{part} sedimentation rate and the N_{part} production below the 9-m depth gave the total flux of sedimenting N_{part} (230 mmol m^{-2} yr^{-1}). This flux was reduced by 74 mmol m^{-2} yr^{-1} as a result of the dissimilative NH_4^+

production below the 9-m depth. The resulting amount of N_{part} finally stored in the sediments was 156 mmol m^{-2} yr^{-1} (74% of the in-lake TN removal) and was in good agreement with the long-term average of N accumulation in the Plešné Lake sediment (Table 3).

(2) NO_3^-: Both assimilation and denitrification were the dominant in-lake sinks of NO_3^-, and we tried to estimate their proportion. If we neglect N_2 fixation by the phytoplankton (*see* below), the total in-lake production of TON originated from NH_4^+ and NO_3^- assimilation. NH_4^+ is usually the primary N source for freshwater phytoplankton (Procházková et al. 1970; Wetzel 2001). We assumed that all NH_4^+ entering the lake (44 mmol m^{-2} yr^{-1}) was assimilated and the NO_3^- assimilation represented 268 mmol m^{-2} yr^{-1} (i.e., 312 − 44 mmol m^{-2} yr^{-1}). The difference between the net in-lake NO_3^- retention (324 mmol m^{-2} yr^{-1}) and NO_3^- assimilation gave 56 mmol m^{-2} yr^{-1} of NO_3^-, which was denitrified. Thus, estimated denitrification represented 26% of the net in-lake TN removal.

The denitrification rate can be also calculated using an N : P ratio method, which is based on changes in the N : P ratios of the net TN and TP retention in the lake ($\Delta TN:\Delta TP$) and of the N and P concentrations in the surface sediments ($N_{sed}:P_{sed}$) (Molot and Dillon 1993). This method assumes that all retained P is stored in sediments, while part of the retained N is removed by denitrification (N_{dnf})

$$N_{dnf} = \Delta TN(\Delta TN:\Delta TP - N_{sed}:P_{sed})/(\Delta TN:\Delta TP) \quad (1)$$

The net in-lake TN and TP retention was 211 and 4.6 mmol m^{-2} yr^{-1}, respectively, with a $\Delta TN:\Delta TP$ ratio of 45.7. The molar $N_{sed}:P_{sed}$ ratio was 25.0 (Table 4). The resulting N_{dnf} (95 mmol m^{-2} yr^{-1}) was almost twice as high as in the previous estimation. This disproportion could be associated with the neglected N_2 fixation, the altered P chemistry in an acidified lake, or uncertainty in the determination of nutrient fluxes.

The fixed nitrogen would reduce the value of NO_3^- assimilation (based on TON balance) and, inversely, would increase the proportion of denitrified NO_3^-. Nitrogen fixation was not measured but it was unlikely, because the cyanobacterial species in Plešné Lake (*Pseudanabena* sp. and *Limnotrix* sp., Oscillatoriales) have no heterocysts. Moreover, they represented <15% of the phytoplankton biomass in the Plešné Lake (Vrba et al. 2003; unpubl. data) and the epilimnetic NH_4^+ and NO_3^- concentrations were low (<2 and <5 μmol L^{-1}, respectively) only in August and September (Fig. 3). Under such conditions, the nitrogen limitation of phytoplankton growth was unlikely (Kalff 2002), and N_2 fixation was probably a negligible TON source in Plešné Lake.

The chemistry of strongly acidified Plešné Lake was altered compared to circumneutral lakes because of P immobilization by colloidal Al_{part} and the elevated P-sorption capacity of sediments (Kopáček et al. 2000). Sedimentation of abiotic P_{part}, as well as the increased P retention in sediments, could lower the sediment N : P ratio compared to that resulting from biotic processes only and, consequently, could overestimate the N_{dnf} flux calculated from Eq. 1.

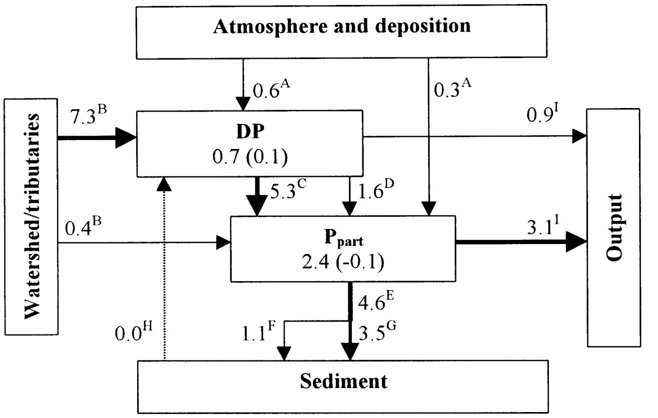
(3) NH_4^+: Ammonium is assimilated by phytoplankton and usually also rapidly nitrified by bacteria under oxic conditions, and its epilimnetic concentrations are commonly low (Wetzel 2001). However, the annual discharge weighted mean NH_4^+ concentration was 5.7 μmol L^{-1} in the Plešné Lake outlet during this study. Such a situation, with one order of magnitude higher NH_4^+ concentrations in the outlet than in the tributaries, has currently been common in all acidified Bohemian Forest lakes (Kopáček unpubl. data). Atmospheric NH_4^+ input partly contributed to this pattern but could not explain why Plešné Lake was a net source of NH_4^+ (Table 2).

Although both NH_4^+ and a part of NO_3^- were assimilated by the phytoplankton, the dissimilation of sedimenting seston and sediment liberated N entirely as NH_4^+. Although nitrification ceased in Plešné Lake as a result of its long-term acidification (pH < 5 for several decades), as described for experimentally acidified lakes (Rudd et al. 1988), both assimilation and dissimilation continued under acid conditions. Because NH_4^+ was not removed from the water column by nitrification, its concentration increased even in the oxic hypolimnetic layers and, during winter, in the whole lake (Fig. 2). If we assume that all NH_4^+ entering the lake was assimilated and that the lake was a net NH_4^+ source (30 mmol m^{-2} yr^{-1}), the total dissimilative NH_4^+ production was 74 mmol m^{-2} yr^{-1}. This result, based on the mass balance approach, corresponded well with the hypolimnetic NH_4^+ production (77 mmol m^{-2} yr^{-1}).

The above results show that the internal NH_4^+ source can exceed its sinks in acidified lakes, which have ceased nitrification and have significant assimilation of NO_3^- (an alternative N source). Plešné Lake has TP and chlorophyll *a* concentrations (maximum values of 0.4 μmol L^{-1} and 50 μg L^{-1}, respectively) that place it among mesotrophic lakes. Acidification has caused this natural water body with low production to behave similarly (considering the ability to produce NH_4^+) to a wastewater treatment plant (i.e., an aquatic system with several orders of magnitude higher nutrient loading).

The in-lake phosphorus cycle—The total in-lake input of TP was 8.6 mmol m^{-2} yr^{-1}, of which 92% was in the dissolved form due primarily to the high DRP concentrations in tributaries (Table 1). On an annual basis, Plešné Lake was a net sink of 88% of DP (6.9 mmol m^{-2} yr^{-1}), which was converted to P_{part}. Biomass production and P immobilization by Al_{part} were two major processes responsible for this DP transformation (Fig. 6). The P_{part} production associated with the biomass growth was estimated using two independent approaches: (i) The total in-lake biotic C_{part} production (4,723 mmol m^{-2} yr^{-1}) and the average epilimnetic $C_{part}:P_{part}$ ratio (Table 4) gave a biotic P_{part} production of 5.7 mmol m^{-2} yr^{-1}. (ii) The total in-lake TON production (312 mmol m^{-2} yr^{-1}) and the average epilimntetic $N_{part}:P_{part}$ ratio (Table 4) gave a biotic P_{part} production of 4.8 mmol m^{-2} yr^{-1}. The average biotic P_{part} production was 5.3 mmol m^{-2} yr^{-1}. The difference between the net in-lake sink of DP and the biotic P_{part} production was 1.6 mmol m^{-2} yr^{-1}, representing DP, which was converted from the liquid to particulate phase by abiotic immobilization with colloidal Al forms.

The abiotic P immobilization significantly (20%) reduced the pool of potentially bioavailable DP. Moreover, the microbial processes dominated pelagic food webs, while higher



A Direct atmospheric input.
B Input by tributaries.
C Biotic production of P_{part}.
D Abiotic production of P_{part} due to P immobilization by colloidal Al.
E Total P storage in sediments (in-lake retention of total P).
F Orthophosphate liberated by dissimilation of sedimenting seston, converted to P_{part} by colloidal Al, and stored in the sediment as inorganic particulates.
G Net storage of the sestonic P_{part} in sediments; the difference between the fluxes (E) and (F).
H Orthophosphate release from sediments; prevented by Al oxyhydroxides.
I Output from the lake by outflow.

Fig. 6. Major fluxes and transformations of phosphorus forms (DP, dissolved P, and P_{part}, particulate P) in Plešné Lake in the 2001 hydrological year. Arrows represent P fluxes (mmol m^{-2} yr^{-1}). Boxes represent pools of P forms (mmol m^{-2}) with annual changes in their storage in the lake (mmol m^{-2} yr^{-1}) given in brackets.

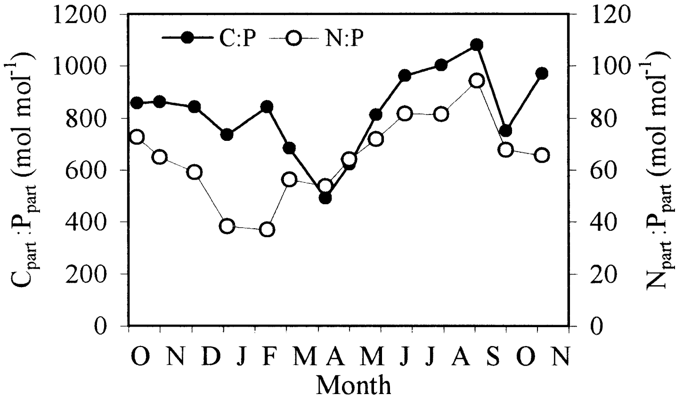


Fig. 7. Seasonal trends in $C_{part}:P_{part}$ and $N_{part}:P_{part}$ ratios of the epilimnetic seston in Plešné Lake in the 2001 hydrological year.

trophic levels were almost absent in Plešné Lake, eliminating a source of biological P recycling typical for nonacidified water bodies. We hypothesize that these patterns led to a severe P limitation of the Plešné Lake phytoplankton despite relatively high P loading (Table 2). The molar $C_{part}:P_{part}$ and $N_{part}:P_{part}$ ratios of the epilimnetic seston were two to ten times higher (Fig. 7) than C : P and N : P ratios of marine plankton, which have been inferred to be indicative of nutrient-sufficient status of plankton (106 and 16, respectively; Redfield 1958). But they were also 1.5 to four times higher than the $C_{part}:P_{part}$ and $N_{part}:P_{part}$ ratios of temperate lakes with P-limited growth of plankton (306 and 24, respectively; Hecky et al. 1993). The composition of airborne particulates in atmospheric deposition entering Plešné Lake was close to the Redfield ratio (Table 4) and could not account for such a disproportion. The P deficiency in the Plešné Lake biomass was also supported by one to two orders of magnitude higher activities of extracellular phosphatases in this acidified lake than in circumneutral lakes (Bittl et al. 2001). Similarly, Nalewajko and Paul (1985) observed significant depressions of photosynthesis and P availability in Al-treated waters in the pH range of five to seven. The acidification-induced decline in P availability thus seemed to be another specific pattern in the nutrient cycling within a strongly acidified lake.

The sum of P_{part} input from external sources (0.7 mmol m^{-2} yr^{-1}) and in-lake biotic and abiotic P_{part} productions was 7.6 mmol m^{-2} yr^{-1}. The annual P_{part} output was 3.1 mmol m^{-2} yr^{-1}, and in-lake P_{part} storage decreased by 0.1 mmol m^{-2} yr^{-1}. The resulting P_{part} stored in the sediments was 4.6 mmol m^{-2} yr^{-1}, which represented 53% retention of TP loading to Plešné Lake. Such retention was within values reported for temperate lakes of similar TP loading and water retention time (Wetzel 2001; Kalff 2002).

The measured P_{part} sedimentation rate was 3.8 mmol m^{-2} yr^{-1} in the 9-m depth. As was the case with Al_{part}, the P_{part} sedimentation rate was lower than its storage in sediments (Table 3) because the sedimentation rate did not include the formation of particulate matter below the 9-m depth. The long-term average P accumulation in the Plešné sediment (5.8 mmol m^{-2} yr^{-1}) was, however, higher than the above two independent estimations. The 2001 storage of C, N, and Al in the Plešné Lake sediments was more comparable with their long-term average accumulation than the respective P flux (Table 3), indicating an additional P source for the lake.

Uncertainty and neglected nutrient fluxes—The deposition of needles from shoreline trees (Psenner 1984), airborne transport of particulate organic matter (Wetzel 2001), and overland flow can represent the missing input of particulate nutrients to the lake, whereas the impact of submersed littoral macrophytes was probably limited because of their small area. The additional organic particles would be a relatively more significant source of P than of N or C for the sediments as a result of their more-effective depletion of NH_4^+ and TIC, while liberated orthophosphate would be chemically converted back to P_{part}.

The additional C_{part} input would further increase the positive difference between the carbon storage and long-term average accumulation in sediments (Table 3). The lower long-term average C accumulation compared to actual storage in the sediments could be explained in part by methane production. Methane-producing bacteria consume organic C when dissolved oxygen and other potential electron acceptors are at low levels (Wetzel 2001). Such conditions were common at the sediment–water interface for most of the study period (Figs. 1, 2). Even though we did not measure methane production during this study, a rough estimate of the magnitude of this flux can be made on the basis of measurements by Anderson et al. (2000). They observed elevated methane concentrations in the Plešné hypolimnion, with a maximum of ~2 μmol L^{-1} above the bottom 4 months after the 1997 spring overturn. Even if we assume that the maximum observed concentration of methane was representative for the whole hypolimnion (below the 4-m depth) and its production was stable throughout the year, the resulting hypothetical methane production was ~30 mmol m^{-2} yr^{-1} (i.e., <2% of the C_{part} storage in the sediments).

Another neglected flux is missing information on nutrient recycling within both pelagic and benthic food webs. Nevertheless, we assume that the role of zooplankton was limited because of their very low biomass (Vrba et al. 2003). The role of benthos was not evaluated because of a lack of quantitative data from this lake. Long-term qualitative data on insect larvae in Plešné Lake, however, indicates a pronounced decrease in their biodiversity during the lake acidification (Vrba et al. 2003). This indicates some possible shift in the role of benthos in nutrient cycling compared to circumneutral lakes.

All studies on nutrient fluxes entail a degree of uncertainty, and this study is no exception. Uncertainties are associated with measured input/output data (i.e., with precision of analytical methods and unstable conditions between samplings), estimated parameters, and with factors not considered in the mass budgets. In general, the magnitude of uncertainty increases inversely with the flux, being highest for minor fluxes obtained as the difference between major fluxes (e.g., nitrification, DOC coagulation, or photochemical mineralization). Direct measurements of these minor (or omitted) fluxes would undoubtedly decrease uncertainty to their estimates. The reasonable concordance between major in-lake nutrient fluxes estimated by different independent methods, however, indicates that the uncertainty and neglected nutrient fluxes likely played only a minor role in the overall C, N, and P balances presented for Plešné Lake.

Comparison of nutrient fluxes in acidic and nonacidic lakes—Many nutrient mass balances have been evaluated in different types of lakes (e.g., Wetzel 2001; Kalff 2002). To highlight the similarities and differences between the strongly acidified Plešné Lake and nonacidic lakes we use here an example of forest lakes in central Ontario for which long-term data exist. We selected four of them (Chub, Crosson, Dickie, and Harp) that had similar TP and DOC concentrations (0.23–0.34 and 317–425 μmol L^{-1}, respectively) as Plešné Lake but positive ANC of 12–68 μeq L^{-1} (Dillon and Molot 1996).

Despite comparable in-lake TP and DOC concentrations, Plešné Lake was exposed to higher loads of these nutrients due to two- to four-fold higher areal water load (Table 5). The lower TP loads led to a lower productivity of the Ontario lakes, characterized by significantly lower chlorophyll *a* concentrations (<5 μg L^{-1}; Dillon and Molot 1996) than in Plešné Lake (Fig. 2). Higher productivity of Plešné Lake resulted in net in-lake production of TON, while 24–32% of the external TON loads were retained in the Ontario lakes.

Other differences between the lakes were caused by severe acidification and nitrogen saturation of the Bohemian Forest. (1) Plešné Lake was exposed to a one–order-of-magnitude higher NO_3^- load, but its in-lake retention was within the range observed for the Ontario lakes. (2) The cessation of nitrification in the long-term acidified Plešné Lake resulted in the net in-lake production of NH_4^+, whereas 76–88% of the external NH_4^+ loads were retained in the Ontario lakes (Table 5). (3) External TP loads of these lakes were 2–20% elevated by internal sources (Dillon and Molot 1996), while orthophosphate release from sediments was prevented in Plešné Lake by colloidal Al. Moreover, the abiotic P immobilization with Al removed ~20% of the potentially bioavailable P from the water column of Plešné Lake. These processes contributed to a severe P limitation of biomass in Plešné Lake. Similar differences from nutrient cycling common for circum-neutral lakes can be expected also in other strongly acidified lakes.

Table 5. Nutrient inputs from external sources (tributaries and atmospheric deposition) expressed on a lake area basis (L; mmol m^{-2} yr^{-1}), areal water load (q_s; m^3 m^{-2} yr^{-1}), and in-lake nutrient retention (R, %), calculated as R = 100(Input-Output)/(Input). Negative R indicates a net production. Data are given for Plešné Lake (this study) and for four central Ontario lakes (Chub, Crosson, Dickie, and Harp; long-term means come from Molot and Dillon 1993; Dillon and Molot 1996, 1997).

	Plešné Lake		Central Ontario Lakes	
	L	R	L	R
DOC	6,913	50	2,410–3,310	37–55
TN	865	26	197–272	36–51
NO_3^-	573	54	46–87	29–67
NH_4^+	44	−52	32–47	76–88
TON	248	−27	82–135	24–32
TP	8.55	53	2.7–6.2	40–84
$TP_{ex + in}$*	8.55	53	3.4–6.3	51–84
q_s	11.7		2.7–5.6	

* $TP_{ex + in}$ is total input of TP into the water column from both external and internal sources.

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