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Regular research paper

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THE EFFECT OF LAKE WATER CHARACTERISTICS ON DECOMPOSITION OF AQUATIC MACROPHYTES

ABSTRACT: *In situ* decomposition of the hornwort (*Ceratophyllum demersum* L.), the buckbean (*Menyanthes trifoliata* L.) and leaf blades of the yellow water lily (*Nuphar lutea* L.) was studied with the litter bag method in three small mid-forest lakes of different pH and nutrient content. Time course of decomposition and of nutrient release from decomposing plant material was best fitted with a logarithm approximation and not by usually used exponential fit. pH of lake waters strongly affected decomposition rates of *C. demersum* and *M. trifoliata*. No effect of nutrient concentrations in lake water or in plant tissues on decomposition was noted for any of the analysed plants. Organic carbon deficit is speculated as a possible reason for the observed pH effect on decomposition rates. Modification of particulate and soluble N:P ratios are underlined as a consequence of different N and P release from decomposing plant material.

KEY WORDS: macrophytes, decomposition rate, pH, nutrients, N and P release

1. INTRODUCTION

Small mid-forest lakes are relatively numerous in Poland, particularly in Masu-

rian (north-eastern Poland) and Pomeranian (north-western Poland) Lakelands. Usually devoid of any water throughflow, mid-forest water bodies are susceptible to land impact in a specific way. Due to the amount and types of terrestrial inputs the lakes may be divided into humic lakes where organic matter of allochthonous origin makes lake waters acidic and into lakes richer in nutrients and of neutral or slightly alkaline pH. The former might be polyhumic with brown turbid waters of extremely low transparency or clear-water lakes devoid of the suspension of humic acids but still of pH below 7. Different physical and chemical properties in these two types of lakes should result in different character of nutrient cycling and trophic relationships. For example, liming of a polyhumic Lake Flosek resulted in the increase of plankton diversity and intensified recycling and decomposition of organic matter there (Hillbricht-Ilkowska *et al.* 1998). Studies on the functioning of acid mid-forest lakes and a comprehensive overview of existing literature can be found e.g. in Hillbricht-Ilkowska *et al.* (1998) and Zdanowski and Hutorowicz (1998).

It is reasonable to expect that production and decomposition of vascular aquatic vegetation (both emergent and submerged) will depend on pH and other lake water properties. It was demonstrated for example that light accelerated the release of dissolved organic matter from littoral detritus (Mans *et al.* 1998), which means that in brown waters of polyhumic lakes the process would go more slowly. Detailed studies on the effect of light on decomposition of leaves and shoots of reed showed (Denward *et al.* 2001) that solar radiation inhibited fungal activity on the surface of plant remains but had no effect on bacterial activity.

The influence of water pH on decomposition rate of macrophytes might express itself indirectly through a different composition of microbial communities and different activity of exogenous enzymes. The published data present contradictory opinions on microbial activity in waters of different pH. The negative impact of acidification on microbial activity was shown e.g. by McKinley and Vestal (1982) or Rao and Dutka (1983) while Schindler *et al.* (1985) did not find such an effect. Travník *et al.* (1994) who also did not find different densities and activities of bacteria in acid and limed waters of Scandinavian lakes suggested that opinions of a negative effects of low pH are based mainly on laboratory experiments or on studies from highly degraded (by industrial inputs) natural systems. But even laboratory experiments have not provided conclusive clues in that matter. The activity of pectin decomposing enzymes was significantly lower in acidic medium while cellulase activity did not depend on pH in experimental decomposition of leaves of *Nymphaea alba* L. (Kok and Van der Velde 1991). Schonenberg *et al.* (1990) showed that water pH exerted more inhibiting effect on the decomposition of lignocellulose from vascular aquatic plants than on the decomposition of algal organic carbon. It seems, therefore, that the question of microbial activity and thus decomposition rate in waters of different pH is still open.

Decomposition rate of vascular aquatic plants is, moreover, a species-dependent characteristics (Harris *et al.* 1995). Vascular plants of humic, acidic lakes are dominated by emergent wetland species while macrophytes of lakes with neutral to

slightly alkaline waters are composed of elodeids and/or nympheids. General rule here is the faster decomposition of submerged plants as compared with emergent or terrestrial plants or their parts (Kok and Van der Velde 1994).

In cited studies (except for Harris *et al.* 1995) the decomposition of plant material is understood as a loss of detritus mass. Similarly important could be, however, the rate of nutrient release from decomposing plants. One might expect that in nutrient-poor dystrophic lakes nutrient release and turnover should be faster than in alkaline and more eutrophic lakes. Such a conclusion could be drawn from the studies of Ogburn *et al.* (1987) on the decomposition of *Eleocharis* sp. at different pH.

Decomposition of vascular plants could be an important source of carbon, nitrogen and phosphorus, particularly in small lakes of an extensive littoral zone (Pieczyńska 1993). In view of different, sometimes contradictory, published data it seems reasonable to test the hypothesis that decomposition of higher plants is slower in acid lakes but nutrient release is faster there than in lakes of alkaline waters of more eutrophic character. A diversity of factors affecting the decomposition rate make the hypothesis testable only during an *in situ* experiment.

2. SITE, MATERIAL AND METHODS

Experiment was carried out in three small mid-forest lakes namely Lake Kruczy Staw, Lake Smolak and Lake Linówko in Masurian Lakeland, north-eastern Poland (Table 1). The first one is a dystrophic but not polyhumic lake of high water transparency (Secchi disc depth around 7 m in the summer) and low phytoplankton biomass. Lake Smolak is a typical polyhumic lake of brown waters of pH around 6. Lake Linówko is a hardwater, slightly alkaline and moderately eutrophic water body.

Table 1. Morphometric and trophic features of studied lakes.

	Kruczy Staw	Smolak	Linówko
Surface (ha)	2.1	9.9	7.0
Maximum depth (m)	8.0	3.0	1.5
Lake status	softwater, dystrophic	softwater, polyhumic	hardwater, moderately eutrophic

Six times in 2001 and nine times in 2002 lake water samples were taken for chemical analysis. Water was sampled in the middle parts of lakes at a depth of 0.5 m in triplicate. Temperature, oxygen concentrations and pH were analysed *in-situ*, chlorophyll, calcium concentrations and various forms of N and P were analysed in the lab. Known volume of lake water was filtered through the Whatman GF/C glass fibre filter for analyses of chlorophyll a in acetone extracts (Golterman 1969). Soluble reactive phosphorus, nitrate-nitrogen, ammonia-nitrogen and calcium were analysed in the filtrate with standard limnological methods of molybdenum blue, phenyldisulphonic acid, phenylhypochlorite method and titrimetric method, respectively (Golterman 1969, Solórzano 1969). Unfiltered lake water samples were used for analyses of total P and total N after primary mineralization in a mixture of nitric and perchloric acid (TP) or with standard Kjeldahl procedure (TN).

Lake Kruczy Staw is surrounded by raised and transitory bogs with four dominating moss species: *Sphagnum cuspidatum* Ehrh. ex Hoffm., *S. apiculatum* Lindb., *S. magellanicum* Brid. and *S. rubellum* Klinggr. A narrow belt of shoreline vegetation is overgrown by sedges *Carex limosa* L., *C. lasiocarpa* Ehrh., *Carex nigra* L. and the buckbean (*Menyanthes trifoliata* L.). No submerged vascular plants were found in Lake Kruczy Staw. Lake Smolak is surrounded by a narrow belt of patchy vegetation dominated by sedges and mosses, in-lake macrophytes are composed exclusively of the yellow water lily (*Nuphar lutea* L.) which overgrows 1/5 of the lake surface and produces on the average 52 g m⁻² dry weight biomass annually. Lake Linówko with steep slopes on its shores has practically no emergent macrophyte vegetation and only a narrow belt of wetland plants. Submerged macrophytes are represented exclusively by the hornwort (*Ceratophyllum demersum* L.) which forms extensive underwater meadows with plant biomass about 445 g d.w. m⁻².

The hornwort (*Ceratophyllum demersum* L.), the buckbean (*Menyanthes trifoliata* L.) and leaf blades of the yellow water lily (*Nuphar lutea* L.) were selected for experiments on plant decomposition. The experiments were carried out with the standard litter bag methods using 15 × 20 cm nylon net bags of a mesh size 1.5 mm. Plant samples

(10–30 g fresh weight per bag) were collected from their natural sites in the beginning of senescence (middle of August – a relatively early period associated with unusually warm summer of 2002), pre-weighed, placed in net bags and dried for 3 h in the air. Then the plant samples (of each species irrespective of their origin) were immersed in water of three lakes c. 1 m below the water table. Separate samples of each plant species were taken to determine initial dry matter content in fresh weight and concentrations of organic matter, total nitrogen and total phosphorus in the beginning of the experiment. At irregular time intervals (usually 2–3 weeks) successive bags (2 of each plant species from each lake) with plant remains were removed, plant remains were dried at 105°C, weighed and grinded for elemental analysis. Most of plant samples of *N. lutea* and *M. trifoliata* decomposed before winter and only the last samples of *C. demersum* were taken from lakes in the next spring after ice out.

Organic matter content in plants and in plant detritus was determined as a loss on ignition at a temperature of 550°C. Pre-weighed plant and detritus samples were mineralised in a mixture of perchloric and nitric acid (1:4 v/v) for phosphorus determinations and with standard Kjeldahl procedure for nitrogen analyses. In resulting solutions nutrient concentrations were analysed with the same methods as those used for P and N analyses in lake waters. All results are presented as percent of the initial dry weight and initial P and N content.

3. RESULTS

3.1. Physical and chemical properties of lake waters

Water temperature did not differ significantly between lakes being relatively high (above 24°C) in July–August (Fig. 1). In the beginning of September it started to decline in a way similar in all three lakes. Waters of lakes differed, however, significantly in pH (Fig. 2). During the first vegetative season in-lake pH variability was relatively low. In the second season, probably due to a high primary production of phytoplankton and thus biological decalcification, pH of waters in Lake Linówko was more variable once exceeding 9. Such maxima were not observed in two dystrophic

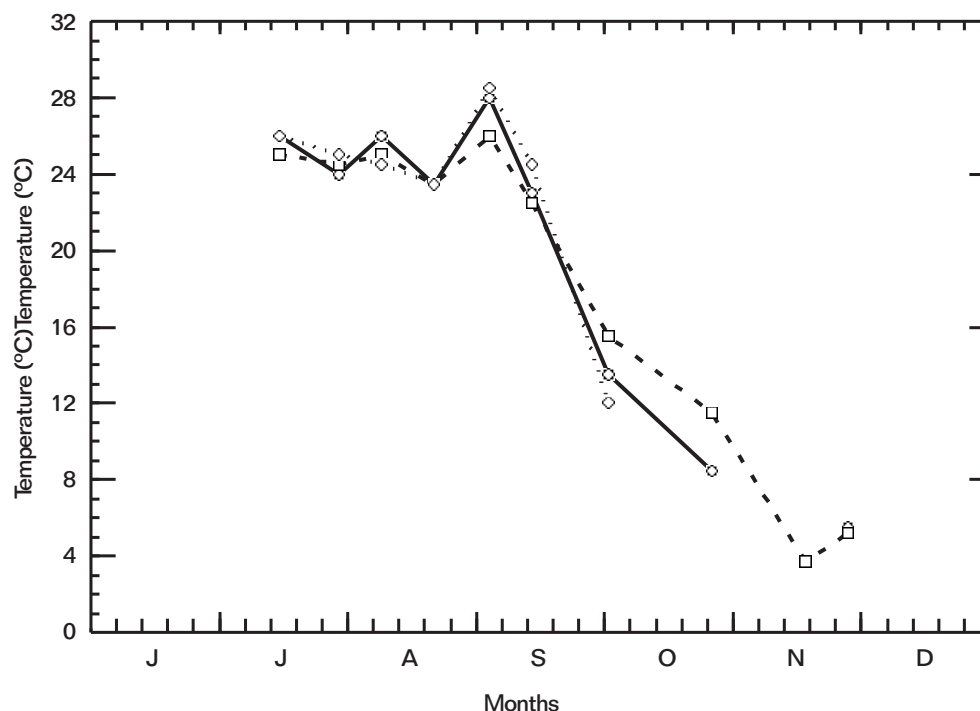


Fig. 1. Water temperature before and during the experiment at a depth of 1 m in Lake Linówko (circles, solid line), Lake Smolak (rhombuses, dotted line) and Lake Kruczy Staw (squares, dashed line).

lakes, probably due to low concentrations of calcium. Between-lake differences in calcium concentrations followed those of pH and were also statistically (t-test) significant (Table 2). No differences, however, were recorded between the lakes in chlorophyll *a* concentrations (Table 2).

Concentrations of soluble reactive phosphorus (SRP) (Fig. 3) and ammonium ions (Table 2) did not differ significantly between lakes. Generally low in all lakes in the summer, SRP markedly increased in the autumn (Fig. 3). Such a regula-

rity was not found in seasonal changes of N-NH₄ concentrations which as a rule did not exceed 0.10 mg N dm⁻³ and varied irregularly during the vegetative season in all studied lakes. Similarly irregular seasonal changes were noted in N-NO₃ concentrations (Table 2). The highest nitrate concentrations were found in waters of Lake Smolak, the lowest – in Lake Kruczy Staw and the differences between the two lakes were statistically significant (t-test).

High irregular seasonal variability was also typical of total phosphorus (TP) and

Table 2. Concentrations of calcium (mg dm⁻³), chlorophyll *a* (mg m⁻³), ammonium-N, nitrate-N, total-N (mg dm⁻³) and total P (mg m⁻³) in waters of three mid-forest lakes (mean for vegetative season ± SD).

Lake	Calcium	Chlorophyll	N-NH ₄	N-NO ₃	TN	TP
2001						
Linówko	64.9 + 8.7	9.4 + 3.9	0.03 + 0.04	0.08 + 0.03	1.15 + 0.34	32 + 17
Smolak	10.3 + 1.5	7.6 + 6.1	0.02 + 0.02	0.11 + 0.06	1.06 + 0.22	39 + 18
Kruczy Staw	5.7 + 1.7	8.7 + 9.6	0.02 + 0.02	0.02 + 0.02	0.51 + 0.29	15 + 11
2002						
Linówko			0.07 + 0.11	0.10 + 0.05	1.00 + 0.38	50 + 31
Smolak			0.06 + 0.05	0.33 + 0.16	1.40 + 0.82	62 + 29
Kruczy Staw			0.04 + 0.03	0.07 + 0.06	0.68 + 0.41	34 + 26

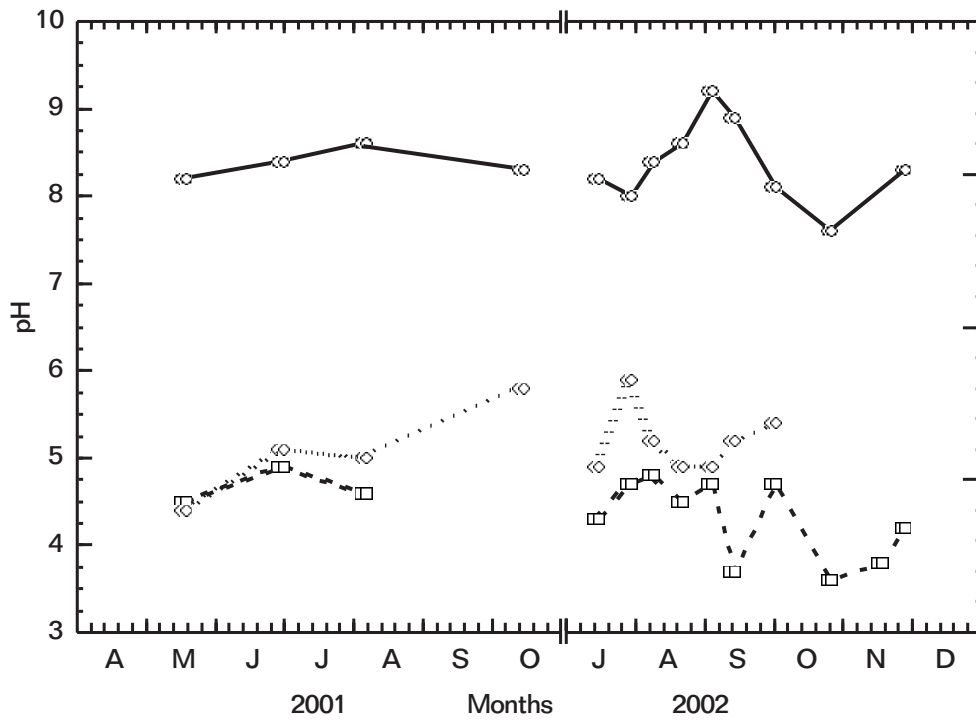


Fig. 2. Seasonal changes of pH in waters of Lake Linówko (circles, solid line), Lake Smolak (rhombuses, dotted line) and Lake Kruczy Staw (squares, dashed line) in 2001 and 2002.

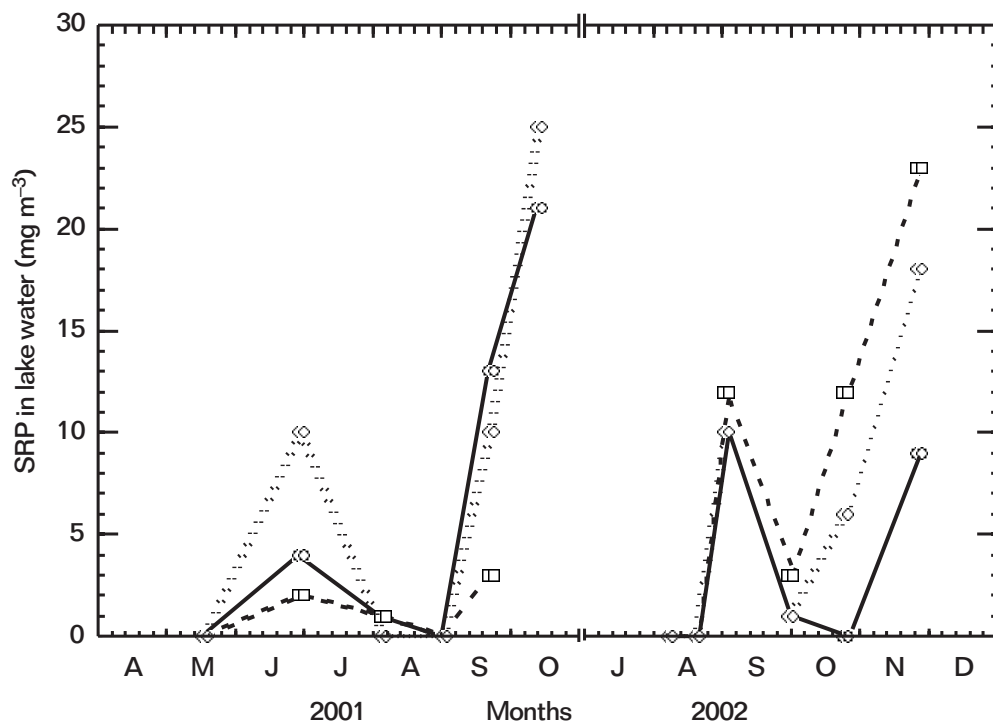


Fig. 3. Concentrations of soluble reactive phosphorus (SRP) in waters of Lake Linówko (circles, solid line), Lake Smolak (rhombuses, dotted line) and Lake Kruczy Staw (squares, dashed line) in 2001 and 2002.

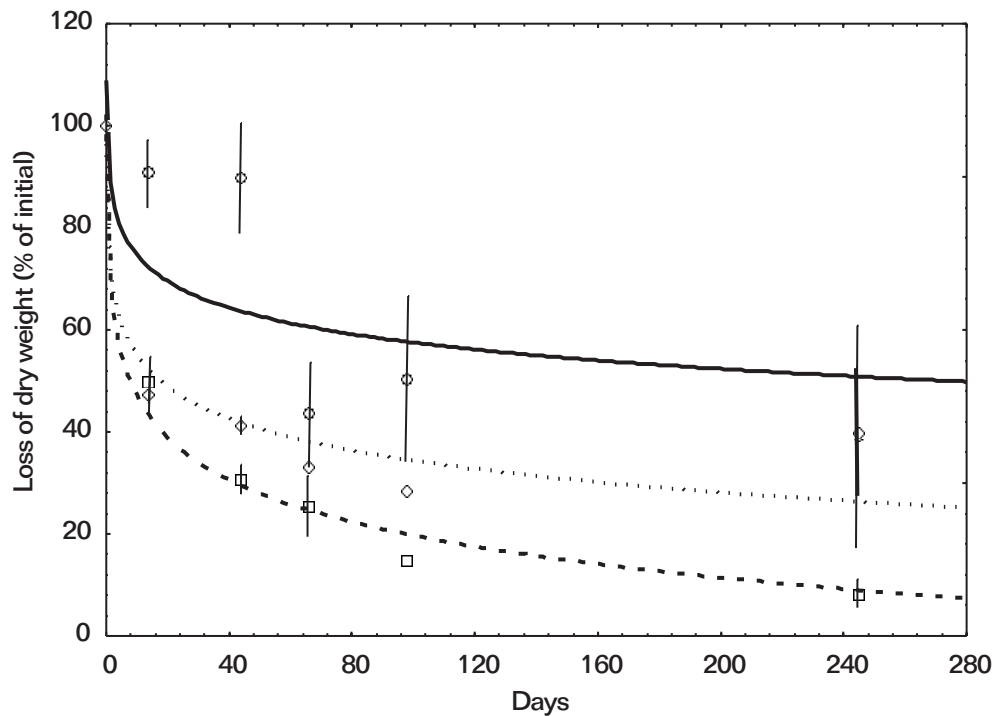


Fig. 4. Losses of dry weight of *Ceratophyllum demersum* plants decomposed in waters of three lakes (Lake Linówko – circles, solid line, Lake Smolak – rhombuses, dotted line and Lake Kruczy Staw squares, dashed line) expressed as percent of initial dry weight (vertical lines denote \pm SD).

nitrogen (TN) concentrations (Table 2). Lakes Kruczy Staw and Smolak differed significantly in TP concentrations and concentrations of total nitrogen in Lake Linówko and Lake Smolak were significantly higher than those in Lake Kruczy Staw. So, albeit markedly different in water pH and calcium content, the lakes were not so clearly differentiated in their trophic status expressed by nutrient and/or chlorophyll *a* concentrations.

3.2. Decomposition of plants and the release of carbon, nitrogen and phosphorus

Measured losses of the plant dry weight during decomposition were best approximated by a logarithm function of time $y = a - b \log t$ where y was expressed as percent of initial plant mass remaining in bags and t – in days (Figs 4–6). Respective non-linear regression equations were statistically significant and well explained temporal variability of plant detritus (R^2 ranging from 0.70 for decomposing leaves of the yellow water lily in Lake Linówko to 0.99 for decomposition of the hornwort in Lake

Kruczy Staw). Logarithm approximation was not significant for only the decomposition of *N. lutea* leaves in Lake Kruczy Staw ($R^2 = 0.52$, $P = 0.069$) and for *C. demersum* plants decomposed in waters of Lake Linówko ($R^2 = 0.57$, $P = 0.081$).

To express instantaneous rate of decomposition we calculated first derivatives of the logarithm function for the days of sampling. Initially high rate of decomposition decreased with time, most probably because of the decrease of water temperature. This relationship is shown here (Fig. 7) for the hornwort, whose decomposition proceeded relatively slow and prolonged for autumn and winter. The respective relationship for leaves of *N. lutea* and for *M. trifoliata* was not statistically significant probably due to a narrow range of lake water temperatures during the subsequent sampling occasions. Data presented in Fig. 7 suggest that decomposition of the hornwort (and probably of other macrophytes) practically ceased at water temperatures below 5–6°C, so during the whole winter time.

For interspecific and between-lake comparisons of the decomposition rate it is more convenient to use some averaged me-

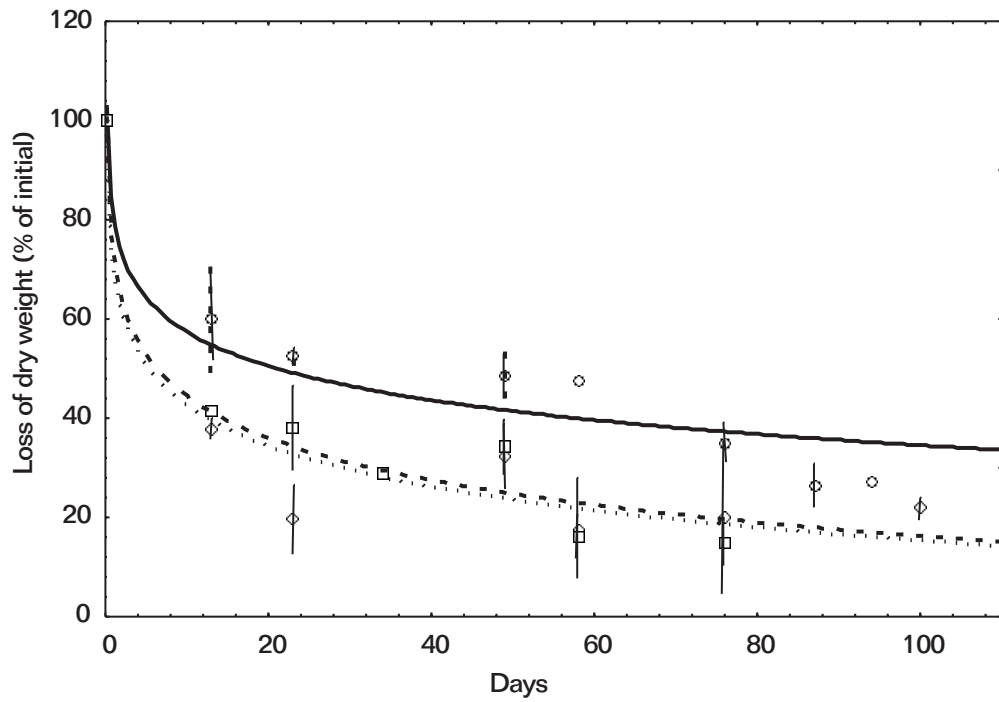


Fig. 5. Losses of dry weight of *Menyanthes trifoliata* plants decomposed in waters of three lakes. Symbols and lines as in Fig. 3.

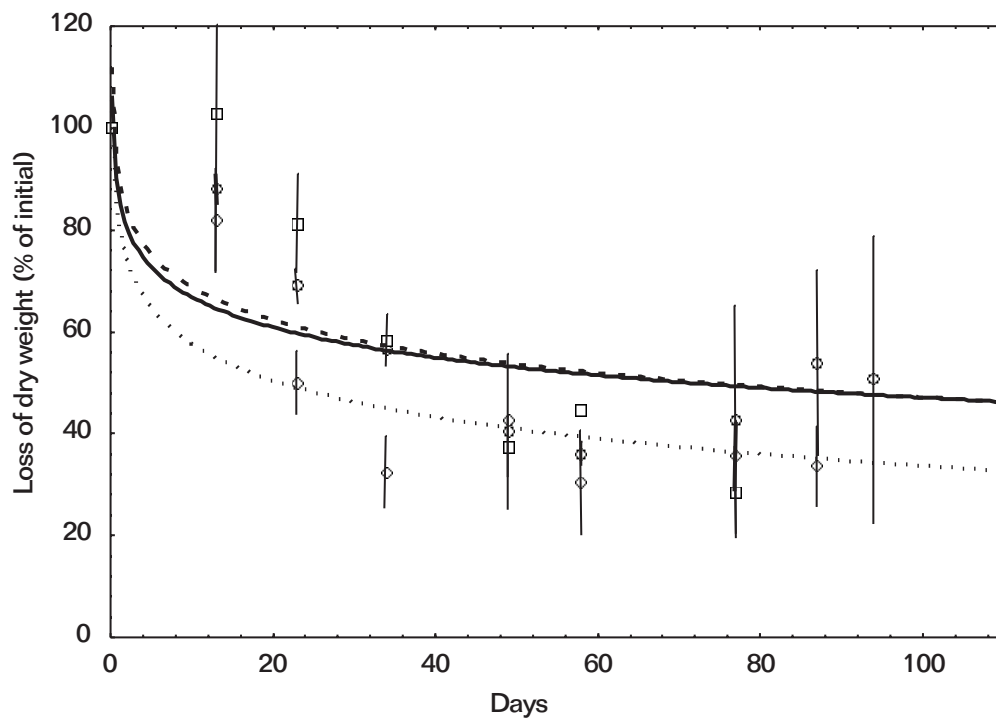


Fig. 6. Losses of dry weight of the leaves of *Nuphar lutea* decomposed in waters of three lakes. Symbols and lines as in Fig. 3.

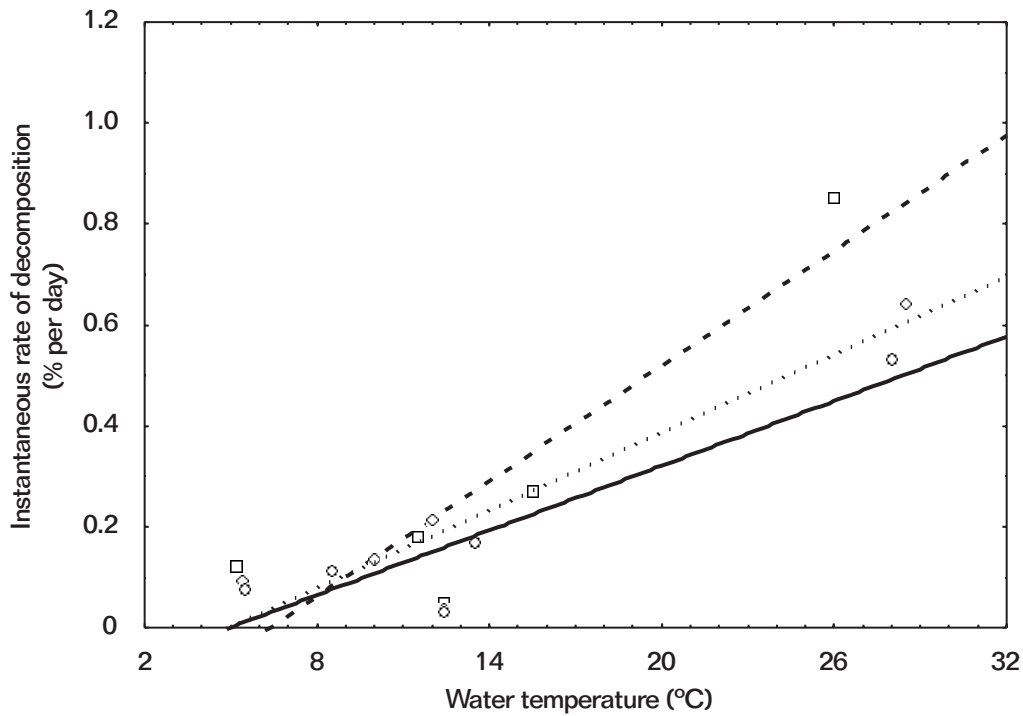


Fig. 7. Instantaneous rate of decomposition (% of dry weight loss per day) of *Ceratophyllum demersum* plants in relation to water temperature. Symbols and lines as in Fig. 3.

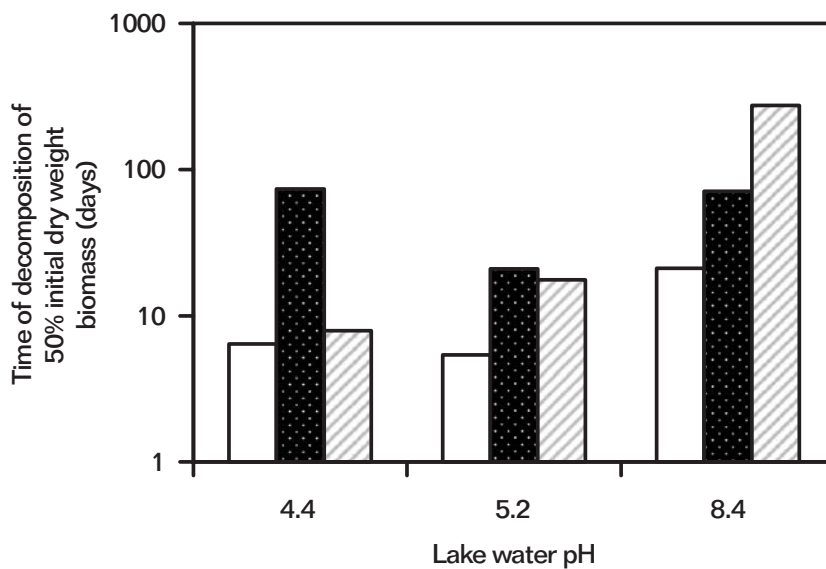


Fig. 8. Time of decomposition of 50% initial dry weight biomass of *Menyanthes trifoliata* (open), leaves of *Nuphar lutea* (dotted) and *Ceratophyllum demersum* (hatched) in waters of different pH.

asures like e.g. the time necessary for decomposition of 50% of the initial plant dry weight. With this approach the rate of de-

composition appeared to be species-specific feature of analysed plants on the one hand and a characteristics dependent of

Table 3. Time required for the release of 50% initial amount of nitrogen and phosphorus from plants (days).

Plant species	Lake Linówko		Lake Smolak		Lake Kruczy Staw	
	N	P	N	P	N	P
<i>Menyanthes trifoliata</i>	53.3	6.7	11.1	2.8	12.5	3.2
<i>Nuphar lutea</i> (leaves)	68.5	8.0	23.4	5.9	a	8.1
<i>Ceratophyllum demersum</i>	a	a	448.4	49.5	62.4	12.4

a – respective logarithm function was statistically insignificant

external factors on the other (Fig. 8). Regardless of the lake, the fastest decomposing plant species was *M. trifoliata* and the slowest – *C. demersum*. pH of lake water had marked effect on the rate of decomposition, most visible for the buckbean and hornwort (Fig. 8). Plants of the two species decomposed significantly faster in acidic waters and the lowest decomposition rate was found in slightly alkaline waters of Lake Linówko. The decay of leaves of the water lily proceeded at a rate irrelevant to pH (Fig. 8).

Since organic matter content (expressed in % of dry weight) did not change significantly during decomposition in any of the analysed plants we may assume that the rate of organic carbon release was nearly identical with that of dry weight losses. The release of nitrogen and phosphorus from decomposing plants occurred, however, at a rate different from that of dry weight losses.

In general, the loss of nitrogen or phosphorus from plants during decomposition was well approximated with a logarithm function $y = a - b \log t$, where y – percent of the initial N or P content in plants at time t . Nonlinear regressions were statistically significant for all experimental variants with the exception of N and P released from the hornwort in Lake Linówko, and of N released from decomposing leaves of the yellow water lily decomposing in Lake Kruczy Staw. Irregularities in the N release were caused by an increase of N content in decaying plant material above the original initial content in the first stage of decomposition. Logarithm relationships explained from 72% (leaves of *N. lutea* in Lake Kruczy Staw) to 99% (*M. trifoliata* in the same lake) variability of P content and from 62% (*N. lutea* in Lake Smolak) to 90% (*M. trifoliata* in Lake Kruczy Staw and *C. demersum* in Lake Smolak) variability of N content in decomposing plant material.

As for dry weight, we calculated an average measure of N and P release from plants i.e. the time necessary to release

50% of the initial nutrient content from plant material (Table 3). Nitrogen was released markedly slower than phosphorus in all experimental variants. The rate of nitrogen release was species-specific – irrespective of external conditions nitrogen was released with the highest rate from *M. trifoliata* and with the lowest – from *C. demersum*. Phosphorus was released from *M. trifoliata* and from leaves of *N. lutea* faster than the rate of dry weight losses of respective plants (compare Table 3 and Fig. 7).

4. DISCUSSION

Decomposition rate of studied macrophytes was best described by the logarithm function. Exponential regression of the type $y = a \exp(-bt)$ where y means the percent of remaining plant mass after time t (often used in such studies – see e.g. Kirchner *et al.* 2001, Menendez *et al.* 2001) gave worse, often statistically insignificant approximation. Better logarithm fit means that the process of decomposition, particularly in its initial phase, proceeded faster than such that could be described by an exponential function. Observed differences could be explained by the fact that our experiment started relatively early (for the reasons described in Methods) and the initial stage of decomposition proceeded in relatively warm lake waters. Consequently, instantaneous rate of decomposition (expressed in % decomposed material per day) decreased during the experiment and could not be characterised by a constant – b as it would be in the exponential process.

Due to methodical differences and specific character of experimental sites any comparison of our results with published data might be not trustworthy. For example, instantaneous rate of decomposition of the hornwort in our experiments varied from 0.0085 per day (Lake Kruczy Staw,

beginning of the exposition) to 0.0003 per day (Lake Linówko, end of the exposition in the spring next year). Similar studies carried out in riverine habitats (Battle and Mihuc 2000) gave the decomposition rate of plants of the same species between 0.049 and 0.008 per day. High rates observed by these authors resulted probably from easy admittance of larger invertebrates (mesh size of the net bags was 5 mm in some experiments) and from the exposition of plant material in running waters. The authors found significant differences in the rate of decomposition between running and stagnant waters.

Obtained results did not confirm the assumed thesis of a slower decomposition of plants in acidic waters. On the contrary, two out of three analysed plant species (*M. trifoliata* and *C. demersum*) decomposed faster in dystrophic, acidic lakes Kruczy Staw and Smolak than in eutrophic Lake Linówko of permanently alkaline waters. Published data on the effect of pH on decomposition of plant material is inconclusive and often contradictory. Schoenberg *et al.* (1990) analysed the decomposition of substrates prepared from algae and from vascular plants in waters of two lakes of different pH and found up to 65% inhibition of the decomposition rate in acidic waters (the effect of pH was different for different substrates). Laboratory experiments in which pH of original lake waters was artificially manipulated demonstrated, however, that variable pH was responsible for only several percent decrease of decomposition rate. The authors suggested that in naturally acidic waters, mobilised heavy metal ions might exert inhibiting effect on the activity of microorganisms involved in decomposition. That effect can probably be excluded from the results presented here. Lake Kruczy Staw and Smolak are situated in catchments that tightly isolate any land impacts and there are no recognisable heavy metal sources in the direct catchment of the lakes.

Limiting effect of pH in Schoenberg's *et al.* (1990) experiments was more expressed for the substrate prepared from macrophytes than for that prepared from algae. Such an effect could be an additional evidence for the commonly agreed thesis that decomposition rate of plants is inversely proportional to the content of cellulose (Webster and Benfield 1986, Belova 1993) or, more general, to the content

of structural parts in decomposing material. Kok and Van der Velde (1991) demonstrated that the activity of three out of four enzymes catalysing components of cell walls in *Nymphaea alba* (polygalacturonase, xylanase and pectin hydrolysing enzymes) were markedly inhibited in low pH. Only cellulase activity did not depend on pH of experimental medium. Schoenberg *et al.* (1990) found, however, significant decrease of the rate of lignocellulose decomposition in waters of low pH. Irrespective of this controversy, cellulose content in our plants (22% in *C. demersum* and 24% in *M. trifoliata* – Bernatowicz 1969) did not differ so as to result in different rates of decomposition.

Analysed plants differed, however, in the initial concentrations of N and P in plant tissues (Table 4). Highest nutrient concentrations were found in *M. trifoliata* plants and the differences in N and P content between the buckbean and two other plant species were statistically (t-test) significant. This factor could explain observed differences in the decomposition rate since plants richer in N and P usually decompose faster. Irrespective of water characteristics *M. trifoliata* decomposed most rapidly among analysed plant species (Fig. 8). Due to a small number of valid cases, no relationship between decomposition rate and the N and/or P content in plants could, however, be demonstrated.

Table 4. Initial concentrations of nitrogen and phosphorus in plant material decomposed in lake waters (mean of 10 plants + SD).

Plant	N (mg g d.w. ⁻¹)	P (mg g d.w. ⁻¹)
<i>Menyanthes trifoliata</i>	29.8 + 9.3	3.64 + 0.43
<i>Nuphar lutea</i> (leaves)	18.6 + 3.6	2.15 + 0.36
<i>Ceratophyllum demersum</i>	19.9 + 1.0	1.94 + 0.54

Unexpectedly high decomposition rate of macrophytes in acidic Lake Kruczy Staw could probably be explained by carbon deficit typical of that water body. Low chlorophyll and high water transparency are the indirect evidence for the lack of organic carbon that might be a substrate for heterotrophic microorganisms. Any allochthonous source of organic carbon might be thus rapidly colonised and decomposed by heterotrophic bacteria and fungi. The latter, under specific circumstances, could be the dominating factor in the decomposition of particulate organic matter (Kuehn *et al.* 2000).

Apart from low pH, waters of dystrophic Lake Kruczy Staw were characterised by low total nutrient concentrations (mean values of two vegetative seasons were 0.61 ± 0.36 mg N dm⁻³ and 26 ± 23 mg P m⁻³ – see Table 3). Highest concentrations of total N and total P were found in Lake Smolak (1.26 ± 0.66 mg dm⁻³ and 52 ± 27 mg m⁻³, respectively) and the differences between two lakes were statistically significant. However, the rates of decomposition of the buckbean and hornwort were similar in both lakes and markedly higher than the respective rates in Lake Linówko (Figs 4, 5 and 8). So, our results did not confirm the hypothesis of the dependence of decomposition rate of macrophytes on lake water fertility.

Nitrogen and phosphorus were released from decomposing material at different rates but generally faster in acidic than in alkaline waters. Irrespective of lake water character, phosphorus was released faster than nitrogen. In some experimental variants detritus nitrogen increased in the initial (decomposition of the hornwort in Lake Linówko and leaves of the water lily in Lake Kruczy Staw) or final (leaves of the water lily in lakes Linówko and Smolak) stage of decomposition. Similar phenomenon, especially in the initial phase of plant decay is known from other studies (Kistritz 1978, Kok and Van der Velde 1994) and explained by colonisation of plant detritus by microorganisms – usually richer in nitrogen than their substratum. At the end of decomposition, apart from this microbial effect, nitrogen could have accumulated due to the fragmentation of detritus particles and surface sorption of ionic forms of nitrogen.

Different rate of the release of N and P from decomposing plants may have important consequences for nutrient cycling in lake ecosystems. It means an increase of the N:P ratio in particles deposited in bottom sediments and relative enrichment of lake waters in recycled P which might further be available for primary producers. Modification of the N:P ratio seems to be a common phenomenon since it manifested itself regardless of the external conditions (composition of lake waters) or of plant species. It could be partially responsible for the observed autumn increase of soluble P in waters of analysed lakes (Fig. 2).

Two conclusions can be drawn from our studies:

- Decomposition rate of aquatic macrophytes is both site-specific and species-specific process. Contrary to many published data we found the highest rates of decomposition in waters of pH <7. The reason was probably an organic carbon deficit in acidic waters though further microbiological studies are needed to test this hypothesis.
- Different rate of N and P release from decomposing plants modifies N:P ratio in settling detritus and in lake waters.

5. SUMMARY

In situ decomposition of the hornwort (*Ceratophyllum demersum* L.), the buckbean (*Menyanthes trifoliata* L.) and leaf blades of the yellow water lily (*Nuphar lutea* L.) was studied with the litter bag method in three shallow (Table 1) small mid-forest lakes – Lake Linówko, Smolak and Kruczy Staw. Assumed null hypothesis was that macrophyte decomposition (in terms of dry weight losses) proceeds faster in alkaline than in acidic waters but nutrient release is more rapid in acid lakes. The lakes had a similar thermal regime (Fig. 1) but differed significantly in pH (Fig. 2) and in calcium but not in chlorophyll concentrations (Table 2). Concentrations of soluble reactive phosphorus – generally low but increasing markedly in the autumn – (Fig. 3) and of ammonium ions (Table 2) did not significantly differ between lakes. Irregular seasonal changes were noted in N-NO₃ concentrations. The highest nitrate concentrations were found in waters of Lake Smolak, the lowest – in Lake Kruczy Staw and the differences between the two lakes were statistically significant (t-test) (Table 2). Lakes Kruczy Staw and Smolak differed significantly in TP concentrations and concentrations of total nitrogen in Lake Linówko and Lake Smolak were significantly higher than those in Lake Kruczy Staw.

Decomposition of three plant species appeared to be both site – and species-specific. The process was best approximated with the logarithm function (Figs 4–6), which explained significant part of dry weight variability during the experiment. *M. trifoliata* was the fastest decomposing plant species regardless of the lake water characteristics. Contrary to the expectations, decomposition of *C. demersum* and *M. trifoliata* plants proceeded faster in acidic than in alkaline waters (Fig. 8). Decay of leaves of *N. lutea* was independent on pH. Temperature exerted a significant effect on decomposition rate which was demonstrated for the hornwort decomposing in three lakes (Fig. 7). The rele-

ase of nutrients from decomposing plant species proceeded with a rate different from that of the dry weight losses. As a rule phosphorus was released faster than nitrogen from decomposing plants irrespective of the plant species. Nutrients were released faster in acidic than in alkaline waters (Table 3). No effect of nutrient concentrations in lake waters or in source plant material on decomposition or nutrient release could be demonstrated though analysed plant species differed in the initial N and P content (Table 4). Neither could we prescribe observed differences to the different content of structural parts of plant material (cellulose).

Rapid decomposition of plant detritus in acidic lakes (and particularly in the clear-water Lake Kruczy Staw) could probably be attributed to organic carbon deficits in this lake though further microbiological studies are needed to support this thesis. Observed differences between N and P release from decaying plant material might affect nutrient cycling in lakes. Relatively faster P release may decrease N:P ratio in water but increase the ratio in sediment deposits.

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6. REFERENCES

- Battle J. M., Mihuc T. B. 2000 – Decomposition dynamics of aquatic macrophytes in the lower Atchafalaya, a large floodplain river – *Hydrobiologia*, 418: 123–136.
- Belova M. 1993 – Microbial decomposition of freshwater macrophytes in the littoral zone of lakes – *Hydrobiologia*, 251: 59–64.
- Bernatowicz S. 1969 – Macrophytes in the Lake Warniak and their chemical composition – *Ekol. pol. Ser. A*, 17: 447–467.
- Denward C. M. T., Anesio A. M., Graneli W., Tranvik L. J. 2001 – Solar radiation effects on decomposition of macrophyte litter in a lake littoral – *Arch. Hydrobiol.* 152: 69–80.
- Goltzman H. L. 1969 – Methods for chemical analyses of fresh waters – Blackwell Scientific Publications, Oxford, Edinburgh, 172 pp.
- Harris T. T., Williges K. A., Zimba P. V. 1995 – Primary productivity and decomposition of five emergent macrophyte communities in the Lake Okechobee marsh ecosystem – *Ergeb. Limnol.* 45: 63–78.
- Hillbricht-Ilkowska A., Dusoge K., Ejsmont-Karabin J., Jasser I., Kufel I., Ozimek T., Rybak J. I., Rzepecki M., Węgleńska T. 1998 – Long term effects of liming in a humic lake: Ecosystem processes, biodiversity, food web functioning (Lake Flosek, Masurian Lakeland, Poland) – *Pol. J. Ecol.* 46: 347–415.
- Kirchner A. K. T., Riegl B., Velimirov B. 2001 – Degradation of emergent and submerged macrophytes in an oxbow lake of an embanked backwater system: implications for the terrestrialization process – *Internat. Rev. Hydrobiol.* 86: 555–571.
- Kistritz R. 1978 – Recycling of nutrients in an enclosed community of decomposing macrophytes (*Myriophyllum spicatum*) – *Oikos*, 30: 561–569.
- Kok C. J., Van der Velde G. 1991 – The influence of selected water quality parameters on the decay rate and exoenzymatic activity of detritus of *Nymphaea alba* L. floating leaf blades in laboratory experiments – *Oecologia*, 88: 311–316.
- Kok C. J., Van der Velde G. 1994 – Decomposition and macroinvertebrate colonization of aquatic and terrestrial leaf material in alkaline and acid still water – *Freshwater Biol.* 31: 65–75.
- Kuehn K. A., Lemke M. J., Suberkropp K., Wetzel R.G. 2000 – Microbial biomass and production associated with decaying leaf litter of the emergent macrophyte *Juncus effusus* – *Limnol. Oceanogr.* 45: 862–870.
- Mans C., Denward T., Tranvik L.-J. 1998 – Effects of solar radiation on aquatic macrophyte litter decomposition – *Oikos*, 82: 51–58.
- McKinley V. L., Vestal J. R. 1982 – Effects of acid on plant litter decomposition in an arctic lake – *Appl. Environ. Microbiol.* 43: 1188–1195.
- Menendez M., Martinez M., Hernandez O., Comin F. A. 2001 – Comparison of leaf decomposition in two mediterranean rivers: a large eutrophic river and an oligotrophic stream – *Internat. Rev. Hydrobiol.* 86: 475–486.
- Ogburn R. W. III, Brezonik P. L., Delfino J. J. 1987 – Effects of pH on phosphorus release during macrophyte (*Eleocharis* sp.) decomposition – *Water Resour. Bull.* 23: 829–832.
- Pieczynska E. 1993 – Detritus and nutrient dynamics in the shore zone of lakes: A review – *Hydrobiologia*, 251: 49–58.
- Rao S. S., Dutka B. J. 1983 – Influence of acid precipitation on bacterial populations in lakes – *Hydrobiologia*, 98: 153–157.
- Schindler D. W., Mills K. H., Malley D. F., Findlay D. L., Shearer J. A., Davies I. J., Turner M. A., Linsey G. A., Cruikshank D. R. 1985 – Long-term ecosystem stress: the effects of years of experimental acidification on a small lake – *Science*, 228: 1395–1401.

- Schoenberg S. A., Benner R., Armstrong A., Sobecky P., Hodson R. E. 1990 – Effects of acid stress on aerobic decomposition of algal and aquatic macrophyte detritus: direct comparison in a radiocarbon assay – *Appl. Environ. Microbiol.* 56: 237–244.
- Solórzano L. 1969 – Determination of ammonia in natural waters by the phenylhypochlorite method – *Limnol. Oceanogr.* 14: 799–800.
- Tranvik L. J., Graneli W., Gahnström G. 1994 – Microbial activity in acidified and limed humic lakes – *Can. J. Fish. Aquat. Sci.* 51: 2529–2536.
- Webster J. R., Benfield E. F. 1986 – Vascular plant breakdown in freshwater ecosystems – *Ann. Rev. Ecol. System.* 17: 567–594.
- Zdanowski B., Hutorowicz A. 1998 – Long term effects of liming and fertilisation in acid dystrophic Lake Smolak – *Arch. Pol. Fish.* 6, 2: 159-185.

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