Degraded Softwater Lakes: Possibilities for Restoration

E. Brouwer^{1,2}
J. G. M. Roelofs¹

Abstract

In the Netherlands, the characteristic flora of shallow softwater lakes has declined rapidly as a consequence of eutrophication, alkalization and acidification. The sediment of most lakes has become nutrient rich and anaerobic. We expected that, if a vital seed bank was still present, restoration of the original water quality and sediment conditions would lead to the return of softwater macrophytes. The restoration of 15 degraded, shallow, softwater lakes in the Netherlands was monitored from 1983 to 1998. In eutrophied as well as in acidified lakes, removal of accumulated organic matter from the sediment and shores was followed by rapid recolonization of softwater macrophytes present in the seedbank. After isolation from alkaline water and subsequent mud removal, this recovery was also observed in alkalized lakes. Further development of softwater vegetation correlated strongly with the water quality. When renewed eutrophication was successfully prevented, softwater macrophytes could expand. However, in acidified lakes, Juncus bulbosus and Sphagnum species became dominant after restoration. Liming of an acidified lake was followed by re-acidification within 3 years. Recolonization by softwater macrophytes was inhibited by high turbidity of the water column and spreading of large helophytes on the shore. As an alternative, controlled inlet of alkaline, nutrient-poor groundwater was studied in a few lakes. The pH of those lakes increased, the carbon and nitrogen availability decreased and softwater macrophytes returned. Successful restoration has contributed considerably to maintaining biodiversity in softwater lakes in the Netherlands.

Key words: ammonium, carbon dioxide, dredging, groundwater, liming, macrophytes, mud removal, softwater lakes.

Introduction

he water column of most softwater lakes is very poor in nitrogen, phosphorus and inorganic carbon. Low carbon availability especially limits macrophyte growth. Bicarbonate is almost absent and less than 50 µmol/L of carbon dioxide is present. Under these circumstances, most submerged aquatic plants are not able to take up sufficient carbon dioxide for net photosynthesis (Sand-Jensen 1983; Roelofs et al. 1984; Maberly 1985; Wetzel et al. 1985). Carbon dioxide concentrations in the sediment pore water are much higher, generally above 500 µmol/L. Especially rosette-forming macrophytes, isoetids, possess adaptations to a limited carbon availability. The adaptations are carbon uptake by an extensive root system, dark fixation, recapture of photo-respired carbon dioxide in an extensive lacunal system and radial oxygen loss by the roots (Wium-Andersen 1971; Wium-Andersen & Andersen 1972; Keeley 1982; Madsen 1985). Sediment oxidation via radial oxygen loss stimulates mineralization and enables the growth of mycorrhizal fungi (Wigand et al. 1998). This oxidized layer acts as a barrier against diffusion of reduced phosphate to the water column and stimulates denitrification (Risgaard-Petersen & Jensen 1997).

Eutrophication, acidification and alkalization (increase of alkalinity or Acid Neutralizing Capacity, ANC) are three common causes of decline of the vegetation of softwater lakes in the Netherlands. Increased nutrient input is a consequence of changed land use in the immediate surroundings or of contact with eutrophied water (Arts & Leuven 1988). The first sign of eutrophication is often an increased growth of caulescent and nymphaeid macrophytes and of algae (Schindler 1974; Roelofs 1983). This leads to shading and disappearance of isoetid macrophytes like Lobelia dortmanna (water lobelia) and Isoetes (quill-wort) species. The enhanced biomass production causes accumulation of organic matter on the sediment, which becomes anaerobic and enriched with nutrients. When the input of nutrients from external sources and via diffusion from the sediment exceeds the uptake by macrophytes and algae, nutrient concentrations also increase in the water column.

Another source of eutrophication can be alkalization. In the Netherlands, large amounts of alkaline water are often used to compensate for water losses. Especially in lakes with peaty sediments, this causes nutrient mobili-

¹Department of Ecology, Research Group Environmental Biology, University of Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands

²Address correspondence to E. Brouwer, email Emiel.Brouwer @inter.nl.net, or J. G. M. Roelofs, email J.Roelofs@sci.kun.nl

^{© 2001} Society for Ecological Restoration

zation from the sediment and disappearance of the softwater vegetation (Smolders & Roelofs 1995; Brouwer et al. 1999). Smolders (1995) found a strong positive correlation between the alkalinity of the water column and the phosphate availability in peaty lakes in the Netherlands. In acidified Norwegian lakes, liming is a common practice (Appelberg 1998; Hindar et al. 1998). A part of the powdered limestone accumulates on the sediment. Especially in annually limed lakes, this leads to alkalization and mobilization of carbon, phosphate and ammonium in the sediment (Roelofs et al. 1994). During periods of re-acidification, *Juncus bulbosus* (bulbous rush) can spread rapidly on such sediments (Lucassen et al. 1999).

A large number of the hydrologically-isolated softwater lakes in the Netherlands have become acidified after decades of acidifying, nitrogen and sulfur-enriched atmospheric deposition (Arts & Leuven 1988). Acidification of softwater lakes leads to periods with higher carbon dioxide concentrations in the water column and dominance of ammonium over nitrate (Roelofs 1983; Rudd et al. 1988). When acidification is a consequence of ammonium deposition, ammonium accumulates rapidly. Isoetid macrophytes predominantly use nitrate (Schuurkes et al. 1986). In nitrate-using terrestrial and aquatic plant species growing in acid environments, ammonium uptake leads to a reduced cation uptake, nutrient imbalances and internal acidification (Salsac et al. 1987; Smolders et al. 1996; De Graaf et al. 1998). Phosphate availability does not increase after acidification. Vigorous growth of *J. bulbosus*, *Sphagnum* (peat-moss) species or algae contributes to the die-back of isoetids (Nilssen 1980; Hultberg & Andersson 1982; Roelofs 1983). Again, organic matter accumulates on the sediment which becomes anaerobic.

The anaerobic, organic, nutrient-rich layer in eutrophied or acidified softwater lakes strongly inhibits the growth of softwater macrophytes. Alhonen (1985) concluded that such a layer also inhibits restoration. Complete removal of the anaerobic layer in softwater lakes in the Netherlands was followed by oligotrophic conditions in the water column and germination and colonization by softwater macrophytes (Roelofs et al. 1996).

Successful restoration of the vegetation of shallow, eutrophied, and in many cases also acidified, softwater lakes depends primarily on the restoration of the abiotic conditions that were present before degradation, particularly a weakly buffered, well aerated and nutrient-poor sediment and water column. We hypothesize that these conditions can be restored by removal of recently accumulated organic matter from both the riparian and aquatic zone, identification and exclusion of the major sources of eutrophication and, if necessary, by restoring the alkalinity to the original level. To test this hypothesis, 15 eutrophied lakes were selected where the re-

cently accumulated organic matter was removed. These lakes can be divided in four groups:

- (1) Eutrophied softwater lakes, where no additional measures were applied ("eutrophied lakes").
- (2) Eutrophied and alkalized softwater lakes, where the alkalinity was reduced after restoration ("alkalized lakes").
- (3) Eutrophied and acidified softwater lakes, where no additional measures were applied ("acidified lakes").
- (4) Eutrophied and acidified softwater lakes, where additional measures against acidification were applied: liming or controlled inlet of nutrient-poor, alkaline groundwater ("acidified, buffered lakes")

No re-eutrophication was expected after exclusion of all known eutrophication sources. In alkalized lakes, this included reduction of the supply of alkaline water. In acidified lakes, we expected no further recovery when no additional measures against acidification were taken. Based on the results in Norwegian lakes, we expected an increase of alkalinity after liming, but also mobilization of nutrients from the sediment and possible luxurious growth of *J. bulbosus*. We expected that controlled inlet of groundwater would lead to restoration of the original water quality and vegetation of softwater lakes.

Methods

Mud Removal

In all the lakes studied, recently accumulated or degraded organic matter was present as a sapropelium layer on the sediment and as a humic layer covered with tall herbaceous and woody plants on the shores. After draining the lake, this organic matter, including all aquatic and terrestrial plant growth, was removed from both shore and sediment by bulldozers and cranes. Damage to the original, undegraded sediment was avoided as much as possible. This measure was carried out in winter and will be referred to as "mud removal." The year of mud removal is mentioned between parentheses in the following sections.

Sampling Sites

All studied lakes were shallow (maximum depth 2 m) and ranged in size from 0.5 to 100 ha (Table 1). They had a fluctuating water table (0.5–1 m/year) and sandy sediments, sometimes mixed with some peat or loam. During the last 10 years before restoration, bulk atmospheric nitrogen deposition, primarily as ammonium sulfate, varied between ±13 kg/ha/year in the coastal

Table 1. Some characteristics of 15 restored softwater lakes in the Netherlands.

Lake	Size (ha)	North Latitude & West Longitude	Vegetation Before Degradation	Degraded Vegetation Before Restoration		
Eutrophied lakes						
Broekse wielen	0.6	51°43′50″, 5°46′00″	Isoetid/Caulescent	Algae/Nymphaeids/ Lemnids		
Griltjeplak	3	53°23′00″, 5°12′30″	Isoetid/Caulescent	Helophytes		
Alkalized lakes		,		F, 100		
Beuven	100	51°24′00″, 5°39′00″	Isoetid	Algae/Nymphaeids Helophytes		
Banen	19	51°16′20″, 5°48′00″	Isoetid	Algae/Nymphaeids/ Helophytes		
Acidified lakes				riciopitytes		
Bieze	0.5	52°14′10″, 5°48′00″	Caulescent	Juncus		
Ronde ven	3	52°25′50″, 7°00′40″	Isoetid	Helophytes/Juncus/ Sphagnum		
Schoapedobbe	0.6	52°97′20″, 6°15′30″	Isoetid/Sphagnum	Sphagnum		
Schoapepoel	0.5	52°97′10″, 6°15′30″	Caulescent	Juncus		
Steenhaarplas	4	52°09′40″, 6°47′00″	Isoetid	Helophytes, Juncus		
Van Esschenven	4.3	51°34′20″, 5°12′30″	Isoetid/Caulescent	Nymphaeids/Juncus		
Acidified, buffered lakes				, 1		
Scherpven	1.4	51°26′20″, 5°13′50″	Isoetid	Juncus		
Goorven	5.0	51°33′50″, 5°12′20″	Caulescent	Nymphaeids/Juncus		
Keyenhurk	17	51°26′30″, 5°14′30″	Isoetid	Juncus, Helophytes		
Rietven	9	52°25′40″, 7°00′30″	Isoetid	Helophytes/Juncus/ Sphagnum		
Witven	1.7	51°34′10″, 5°12′30″	Isoetid/Caulescent	Nymphaeids/Juncus		

Juncus = Juncus bulbosus (bulbous rush). For classification, see Introduction.

dunes surrounding Lake Griltjeplak to ±21 kg/ha/year near most other, inland lakes (Houdijk & Roelofs 1991).

Eutrophied Lakes. Lake Broekse Wielen (1991) and Lake Griltjeplak (1991) are isolated lakes with fluctuating water levels, fed by moderately buffered groundwater. Under these circumstances, softwater macrophytes are restricted to shallow, incidentally emerging parts. Lake Broekse Wielen received an increasing nutrient load from its agricultural surroundings. In 1980, a strip of 300 m around the lake was added to the nature reserve and thus acted as a buffer against eutrophication. However, the water quality of the lake did not improve. A small part in the center of the lake was left unrestored. In Lake Griltjeplak, water level fluctuations were artificially reduced, causing anaerobiosis of the sediment and mobilization of nutrients. The original hydrology was restored after mud removal. In both lakes, eutrophication had accelerated the natural succession rate and the invasion by helophytes and shrubs.

Alkalized Lakes. Lake Banen (1993) and Lake Beuven (1986) were alkalized and eutrophied after inlet of alkaline brook- and riverwater. In Lake Banen, the supply of alkaline water was completely ended 4 years before mud removal. Only the central part and the eastern shore were restored, and a degraded peat layer was not completely removed (Brouwer et al. 1999). To prevent

acidification, Lake Beuven still received small amounts of alkaline, but nutrient-poor, brook water after mud removal.

Acidified Lakes. Six isolated lakes were both acidified and eutrophied as a consequence of ammonium deposition and accumulation, and no additional measures were applied after mud removal: Lake Bieze (1990), Lake Ronde ven (1994), Lake Schoapedobbe (1990), Lake Schoapepoel (1991), Lake Steenhaarplas (1990) and Lake Van Esschenven (1996). The latter was and is still surrounded by pine plantations, while the other lakes are situated in open moorland. Lake Schoapepoel and Lake Schoapedobbe were not drained before mud removal.

Acidified, Buffered Lakes. To five other acidified and eutrophied lakes, additional measures against acidification were applied. Liming was carried out in Lake Scherpven (1992) only, a very shallow (<0.5 m), isolated moorland pool. In the winter following mud removal, 1.4 ton/ha of powdered limestone was manually added to the water column. After 1 year, 0.35 ton/ha of sodium carbonate was added. A supply of alkaline, nutrient-poor groundwater was realized in four lakes by pumping up deep groundwater from local aquifers. Lake Keyenhurk (1992) and Lake Rietven (1994) are two moorland pools. Lake Goorven (1996) and Lake Witven (1996) are rather deep lakes (2 m), with steep shores

covered by wood. After isolation from alkaline surface water, these four lakes gradually acidified (van Dam & Buskens 1993; Brouwer & Roelofs 1998). The alkalinity of the groundwater varied between 2 and 3 meq/l and nutrient concentrations were low. The inlet usually took place during periods with high water tables in winter and was discontinued when the alkalinity in the lake reached a level of 0.4 meq/L. Lake Witven did not receive groundwater directly, but was connected via a ditch to Lake Goorven and thus received large amounts of weakly buffered water.

Analytical Measurements

With intervals of 3 to 4 months, we collected surface water samples in one liter polyethylene bottles without air space. In the year after restoration, we sampled every 2 months. No samples could be collected during periods of extreme drought. We started the sampling 1 to more than 5 years before restoration, except in Lake Bieze and Lake Steenhaarplas, where we did not start sampling until after restoration. After storage overnight at 4°C, alkalinity was determined by titration of 100 ml of water with 0.01 N HCl down to pH 4.2 and acidity by titration of 100 ml of water with 0.05 N NaOH up to pH 8.2. Because all lakes except Lake Scherpven had a clear water column, the contribution of humic acids to the acidity was negligible. Therefore, the carbon dioxide concentration in the clear lakes was derived from the acidity by correction for pH. A part of each surface water sample was filtered through a Whatman GF/C filter (pore size 1.2 μm). After filtration, the reduction in water clarity due to the presence of humic acids was measured with a Shimadzu 120-01 spectrophotometer (Kyoto, Japan) as the extinction at 450 nm. After adding 10 mg citric acid to avoid precipitation of metals, 50 ml samples were stored at -20°C until analysis. The concentrations of ortho-phosphate (Soluble Reactive Phosphorus, SRP) and nitrate and ammonium were measured colorimetrically with Technicon AA II systems (US), using ammonium-molybdate (Henriksen 1965), hydrazinesulphate (Technicon 1969) and salicylate (Kempers & Zweers 1986), respectively.

Data Analyses

Time series before and after restoration in individual lakes (Table 2) were analyzed using a Wilcoxon signed rank test for related samples, after randomizing both data sets. Data from the first few months after restoration were excluded to avoid interference with the short-term effects of disturbance after mud removal. The effect of groundwater inlet after mud removal on the nitrogen availability was tested using a General Linear Model for repeated measures. For all analyses, SPSSWin, version 7.5 was used.

Results

In this section, the development of vegetation and water quality in each lake following restoration is described. Common trends are described for groups of lakes. An overview is given in Tables 1 and 2, and explained in more detail below.

Eutrophied Lakes

Lake Broekse Wielen. Before restoration, periods with high concentrations of Soluble Reactive Phosphorus (SRP) in the water column occurred at irregular intervals. In the 6 years following mud removal, the SRP concentration remained low. Periods with algal blooms were frequent before restoration and were restricted to autumn and early spring after restoration. Softwater macrophytes quickly established in the water column and the riparian zone. After this, the vegetation remained dominated by many softwater macrophytes, except in the center, where nymphaeid macrophytes dominated the remaining muddy sediment (Fig. 1).

Lake Griltjeplak. As in Lake Broekse Wielen, periods with high SRP concentrations and algal blooms were no longer observed after restoration. Nitrogen and phosphorus availability decreased after restoration, but not significantly (Table 2). Establishment and slow expansion of softwater macrophytes lead to a thin cover of macrophytes (<50%) within 3 years. During periods with low water tables (<0.1 m) in Lake Griltjeplak, the alkalinity of the remaining water column became very high. After this, *Chara* species dominated temporarily. Seven years after restoration, re-eutrophication remained limited to the accumulation of some organic matter on wind-sheltered, relatively deep parts.

Alkalized Lakes

Lake Beuven. Almost continuously high SRP concentrations were observed before mud removal. Restoration was quickly followed by dealkalization and stabilization of SRP concentrations on a low level (Table 2). On a few occasions, an excessive amount of alkaline, nutrient-poor water entered the lake, after which phosphate availability increased and algal blooms occurred (Fig. 2 and Roelofs et al. 1996). During the first year after restoration in 1986, almost all of the 19 species of softwater macrophytes that were formerly observed in Lake Beuven were again present. In the central parts of the lake, the sediment became quickly covered by a dense mat of *Littorella uniflora* (shore-weed) and *Elatine hexandra* (waterwort). The other species primarily occurred in the

Table 2. Some characteristics of 15 restored softwater lakes in the Netherlands.

	Dominant Water Column Before Restoratio			oration	Water Column After Restoration								
Lake	Macrophytes After Restoration	(+/0/-)	N	рН	Alk	CO_2	NH_4	SRP	рН	Alk	CO_2	NH_4	SRP
Eutrophied lakes													
Broekse wielen	Isoetids/ Caulescents	10/1/0	5/13	7.6	747	65	7	0.43	7.7	561	30	17	0.10
Griltjeplak	Isoetids/ Caulescents	7/0/0	7–9/11–14	7.2	1103	87	4.3	0.34	8.0	1669	89	12	0.21
Alkalized lakes	Cudioscorio												
Beuven	Isoetids	17/0/0	21/77-82	7.4	514	_	30	1.76	5.7**	139**	156	14	0.39**
Banen	Isoetids/ Caulescents	15/2/1	18/27–31	7.1	898	193	49	1.0	5.6**	97**	135	19	0.31*
Acidified lakes													
Bieze	Juncus (Caulescents)	1/3/0	0/4–5	-	-	-	-	-	4.1	2	97	12	0.16
Ronde ven	Juncus (Isoetids)	1/3/0	14–17/30	4.5	21	123	185	0.15	4.1	15	105	67**	0.09
Schoapedobbe	Sphagnum	1/1/1	4/25-29	4.7	17	148	158	0.11	4.5	24	88	35**	0.53
Schoapepoel	Juncus (Caulescents)	1/2/0	1/14–15	5.7	99	106	13	0.2	4.6	29	107	37	0.30
Steenhaarplas	Juncus	0/3/0	0/16-18	_	_	_	_	_	4.4	22	223	55	0.42
V. Esschenven Acidified ,	Juncus	2/3/0	28/14–17	5.5	83	192	71	0.19	4.8	40	141	53	0.20
buffered lakes													
Scherpven	Juncus/ Caulescents	4/0/0	1/31–35	4.0	0	169	87	0.29	5.2	80	158	40	0.62
Goorven	Juncus/ Caulescents	6/2/0	23/14–16	5.1	65	264	127	0.23	5.4	72	79**	28**	0.23
Keyenhurk	Juncus/ Isoetids	5/2/0	2–3/11–13	3.9	0	154	178	0.42	5.9*	130*	110	41	0.32
Rietven	Isoetids/ Juncus	5/1/0	16/24–34	4.5	18	100	98	0.09	5.1**	108**	143	52	0.35
Witven	Junc./Caul./ Isoet.	4/1/0	27/10	4.5	33	345	161	0.17	5.4*	72*	135**	28**	0.23

Juncus = $Juncus \ bulbosus. + /0/- = number of species of softwater macrophytes increasing (+), stable (0) or decreasing (-) comparing before and after restoration. N = number of observations before/after restoration.$

riparian zone. In 1999, 13 years after restoration, this pattern was still present.

Lake Banen. Isolation of the lake was followed by a dry summer, causing almost complete desiccation in 1990. After this, the SRP concentration and alkalinity decreased sharply (Table 2). Some softwater macrophytes established locally. After partial mud removal, SRP concentrations in Lake Banen stabilized at a low level, though not as low as in the completely restored Lake Beuven (Fig. 2). The lake was quickly colonized by softwater macrophytes, but strong yearly fluctuations in the vegetation composition were observed. Echinodorus repens (lesser water-plantain), E. hexandra, Eleocharis acicularis (slender spike-rush), the charophyte Nitella translucens and the moss Drepanocladus fluitans were the dominant species. The isoetid species Luronium natans (floating water-plantain), L. uniflora and Isoetes echinospora (quill-wort) declined after initial reestablishment. Sources for re-eutrophication were the unrestored parts, the large numbers of waterfowl and leafinput from the adjacent birch-forest.

Acidified Lakes

Before restoration, the ammonium concentration in the water column of the acidified lakes fluctuated and occasionally reached levels up to 400 μ m/L in most lakes. During the years following mud removal, the nitrogen availability in the water column decreased somewhat (Fig. 3A, dotted lines). However, ammonium remained the dominant source of nitrogen in these lakes (Fig. 3B). SRP concentration remained low (\pm 0.2 μ m/L). The pH did not rise and the carbon dioxide concentrations decreased slightly. In most lakes, a quick spreading of *J. bulbosus* and *Sphagnum* species in the first year after restoration was followed by a gradual decline of these species, correlated with a decrease of carbon dioxide, ammonium and, to a lesser extent, other ion concentrations

JUNE 2001 Restoration Ecology

^{* =} p < 0.05, ** = p < 0.01. Alk. = Alkalinity (μ eq/L), CO₂ = carbon dioxide (μ mol/L), NH₄ = ammonium (μ mol/L), SRP = phosphate availability (O-PO₄, μ m/L). For classification, see introduction.

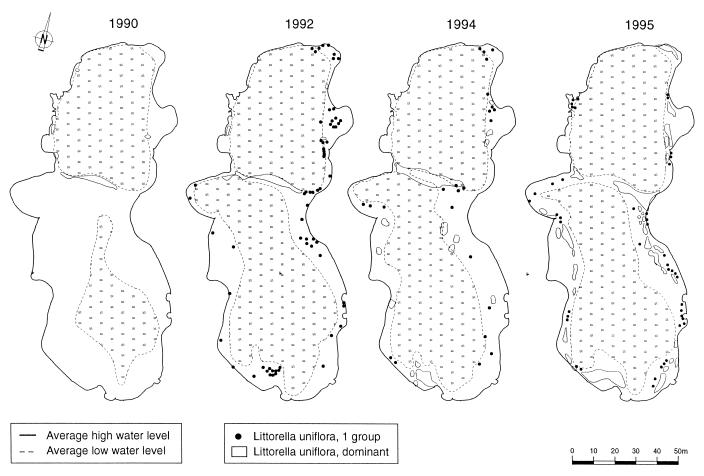


Figure 1. Expansion of *Littorella uniflora* (shore-weed) vegetation after mud removal in the shallow parts of Lake Broekse Wielen (eutrophied) at the end of 1991.

in the water column. Also, some softwater macrophytes established after mud removal, but most of these populations disappeared or declined again between 2 and 5 years after restoration. Isoetid species were often restricted to sites with periodic inflow of acid, superficial and local groundwater.

Lake Bieze. The water column was nutrient-poor but very acidic after restoration in 1990 (Table 2). Some softwater macrophytes established, as well as *J. bulbosus* and *Sphagnum* species. These became dominant, but softwater macrophytes remained present on sites with local inflow of (acid) groundwater. Between 1990 and 1998, this vegetation pattern remained relatively unchanged. In the riparian zone, slow expansion of heather and grasses was observed.

Lake Ronde Ven. The ammonium concentration in the water column decreased significantly after restoration (Table 2). However, Lake Ronde Ven remained acid. Before and after restoration, small populations of *Littorella uniflora* and *Lobelia dortmanna* persisted on sites with su-

perficial groundwater inflow (Table 3). Both species were rarely observed on restored parts, where *J. bulbosus* slowly increased. Seedlings of *Sparganium angustifolium* (floating bur-reed) were observed in the first year, but disappeared after several months.

Lake Schoapedobbe. After restoration in 1990, *Sphagnum denticulatum* quickly became the dominant species again. No softwater macrophytes returned, but the population of *Luronium natans* somewhat increased on sites where the sediment was not acidifed (data not shown) and *Sphagnum denticulatum* was absent. In the riparian zone, a well-developed moor-vegetation from wet soils established. In the period 1993–1997 no structural changes in water quality and vegetation composition were observed, except a decrease of ammonium concentrations (Table 2).

Lake Schoapepoel. After restoration in 1991, *Scirpus fluitans* (floating scirpus), *Potamogeton polygonifolius* (bog pondweed) and *J. bulbosus* became the dominant macrophytes. Also, *Sparganium angustifolium* established. How-

4

5

jan-86 jan-88 jan-90 jan-92 jan-94 jan-96 jan-98

A: Lake Banen

B: Lake Beuven

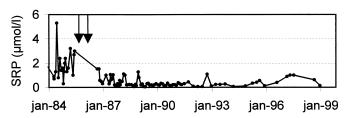


Figure 2. Soluble reactive phosphorus in the water column after isolation from alkaline surfacewater and mud removal in Lake Beuven and Lake Banen. Arrows indicate the time of isolation and subsequent mud removal. Part of the observations on Lake Banen between 1986 and 1990 are obtained from the Limburg Water Pollution Control Authority.

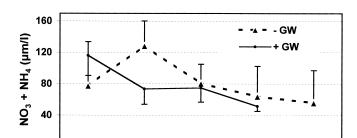
ever, in the following years, *Scirpus fluitans* and *Potamogeton polygonifolius* gradually disappeared. After 1995, *J. bulbosus* was the dominant macrophyte and *S. angustifolium* remained present in a muddy corner of the lake.

Lake Steenhaarplas. After restoration in 1990, Littorella uniflora and Lobelia dortmanna re-established during dry periods. Both isoetid species disappeared again during prolonged periods with high water tables in 1994 and 1995. J. bulbosus was especially abundant during the first 2 years after restoration and after periods with high rainfall. Sphagnum species were the only other macrophytes present in the water column.

Lake Van Esschenven. After restoration in spring 1996, several softwater macrophytes seedlings (*Potamogeton gramineus* (various leaved pondweed), *Pilularia globulifera* (pillwort), *Potamogeton polygonifolius*, *Hypericum elodes* (St. Johns-wort) and *Luronium natans* were found. Of these, only some *H. elodes* and *L. natans* established at a few sites in the small riparian zone after acidification in the summer of 1996. In 1998, instream of slightly alkaline water from the nearby Lake Witven ended this acidification.

Acidified, Buffered Lakes

Lake Scherpven. In the first months after liming of this lake, the pH increased to 7. But, during the 4 years fol-



3

years after mud removal

2

0

1

A: NO3 + NH4

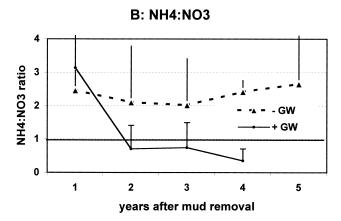


Figure 3. Nitrogen availability in the water column of acidified, ammonium-enriched softwater lakes after mud removal. -GW = Without additional measures against acidification (Lake Keyenhurk before 1996, Lake Ronde ven, Lake Schoapedobbe, Lake Schoapepoel and Lake Steenhaarplas). +GW = With subsequent supply of groundwater (Lake Rietven, Lake Goorven, Lake Witven, Lake Keyenhurk after 1995). The difference between the two groups was not significant (N + N, p = 0.62, N:N ratio, p = 0.12).

lowing liming, the pH gradually decreased again to 4.5. The water column became extremely colored by humic substances, initially limiting light penetration to the upper 20 cm (Fig. 4). Therefore, virtually no aquatic macrophyte growth was observed during these years. On the shoreline, however, several amphibian softwater macrophytes established (e.g., *P. globulifera* and *H. elodes*). After several years, *Juncus effusus* (soft rush) started to spread rapidly on sites where lime had accumulated, suppressing the softwater macrophytes (Fig. 5). Average SRP concentrations in the lake and in the sediment pore water on limed spots were relatively high after liming; 0.62 and 1.06:m/L, respectively.

When mud removal in acidified lakes was followed by a controlled supply of small amounts of alkaline groundwater in winter, pH and alkalinity increased to

JUNE 2001 Restoration Ecology

Table 3. Estimated abundance of softwater macrophytes after mud removal in Lake Ronde ven (acidified) in winter 1993/1994 and after mud removal and groundwater inlet in Lake Rietven (acidified, buffered) in winter 1993/1994. In Lake Ronde ven, a small growth site of *Lobelia dortmanna* and *Littorella uniflora* was not restored. Abundance expressed as number of rosettes or shoots or as sediment surface area where species dominates the vegetation.

	1993	Rest.	1994	1995	1996	1997	1998
Lake Ronde ven, unrestored:							
Lobelia dortmanna (rosettes)	250	50	186	201	10	130	600
Littorella uniflora (m²)	100	100	100	100	20	5	20
Lake Ronde ven:							
Lobelia dortmanna (rosettes)	0	0	0	0	0	5	20
Littorella uniflora (m²)	0	0	0.1	0.1	0.1	0.1	5
Sparganium angustifolium (shoots)	0	0	6	2	0	0	0
Lake Rietven:							
Lobelia dortmanna (rosettes)	0	0	0	13	0	325	3000
Littorella uniflora (m²)	800	0	1	2	5	100	300
Pilularia globulifera (m²)	0	0	0	0	0	0	5
Sparganium angustifolium (shoots)	0	0	1	20	20	30	40

Rest. = immediately after restoration.

levels normal for softwater lakes. In Lake Rietven, Lake Goorven, Lake Witven and Lake Keyenhurk, the pH varied between 6 and 7 after inlet. In the first years after restoration, the pH gradually declined to values between 4.5 and 5 in autumn. After this, groundwater was supplied again, mostly during winter. Immediately after groundwater supply, the carbon dioxide availability in the water column decreased sharply (Table 2, Fig. 6). Ammonium concentrations decreased more slowly, but further than in restored lakes without groundwater supply (Fig. 3). Some phosphate mobilization occurred after groundwater inlet, but not above levels characteristic to softwater lakes. After wet periods with superficial, acidified groundwater influx, both the ammonium

and the carbon dioxide levels increased again and pH decreased. *J. bulbosus* and *Sphagnum* species often became more abundant in such periods. During the first few years with repeated groundwater supply, the average carbon dioxide and nitrogen availability decreased and nitrogen was predominantly present as nitrate (Fig. 3). The turbidity increased somewhat for a few months, only after the first supply of groundwater.

Lake Goorven. After restoration, reestablishment of softwater macrophytes was limited to shallow parts of the lake. Acidification in the summer of 1996 was prevented by the inlet of groundwater. This inlet was fol-

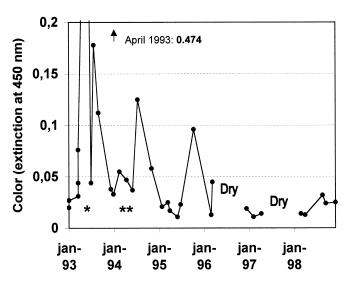
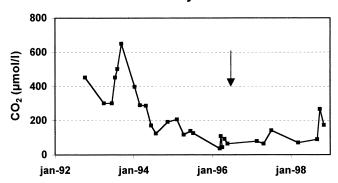


Figure 4. Light absorption by humic acids in Lake Scherpven after liming (*) and sodium carbonate addition (**).

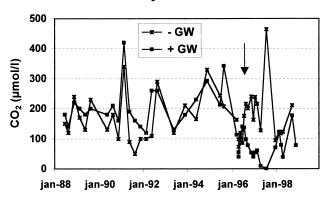


Figure 5. Lake Scherpven, 5 years after mud removal and liming, during a period with low water table. Softwater macrophytes are still present (not visible), but a rapid spread of *Juncus effusus* (soft rush) occurs. Background: Moor vegetation dominated by grasses as a consequence of nitrogen deposition.

A: Lake Keyenhurk



B: Oisterwijkse vennen Lakes



C: Bergvennen Lakes

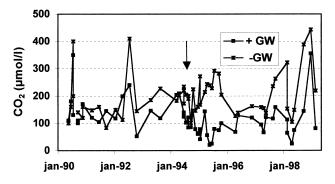


Figure 6. Long-term trends in carbon dioxide availability and the impact of controlled supply of alkaline groundwater in Lake Keyenhurk, the Oisterwijkse vennen Lakes (Lake Goorven versus Lake Van Esschenven), and the Bergvennen Lakes (Lake Ronde ven versus Lake Rietven).

lowed by a decline of *J. bulbosus* and to a lesser extent caulescent softwater macrophytes in the following years. Some isoetids established in this period (*Littorella uniflora, Echinodorus repens*), but due to the steep shores, vegetation was limited to a small zone. Locally, needles from the surrounding pine forests accumulated again on the sediment.

Lake Keyenhurk. After restoration, *J. bulbosus* and *Sphagnum* species formed a dense mat throughout the lake. *Littorella uniflora* and *Ranunculus ololeucos* were still present, but gradually declined further in the acid water column. The start of the inlet of alkaline groundwater in 1996, 4 years after restoration, was followed by a rapid expansion of *L. uniflora* and by the establishment of *Pilularia globulifera*, *Potamogeton polygonifolius* and *Hypericum elodes*. Dominance of *J. bulbosus* and *Sphagnum* species became more local and more periodic.

Lake Rietven. Restoration was followed by the start of the inlet of groundwater in summer 1994. *L. dortmanna* established in 1994, but was not observed during the dry summers of 1995 and 1996. After these years, a rapid expansion followed, resulting in a population of more than 10,000 individuals in 1999 (Table 3). Five years after restoration, the dominant macrophytes were *Eleocharis palustris* (common spike-rush), *E. multicaulis* (many-stemmed spike-rush), *Littorella uniflora*, *Lobelia dortmanna* and *J. bulbosus*. Total cover was less than 50%. Increased helophyte growth indicating alkalization and eutrophication of the sediment was restricted to the point where alkaline water entered the lake.

Lake Witven. During the year following restoration, carbon dioxide and ammonium availability in the water column was very high. In this period, the lake became densely covered by *J. bulbosus*. Softwater macrophytes established primarily in the riparian zone. In the following years, the *J. bulbosus* cover gradually declined, especially after the inlet of slightly alkaline water from Lake Goorven at the end of 1996. Softwater macrophytes did not increase further. Locally, a rapid accumulation of organic matter occurred, due to the input of needles from pine trees overhanging the steep riparian zone.

Discussion

Colonization After Mud Removal

In all lakes, a rapid colonization of the bare sediment was observed during the first year after mud removal. This fast recolonization and the fact that recolonization was limited in all cases to species that were present in the recent past but often absent in the years before restoration, suggested the presence of a vital seed bank (Roelofs et al. 1996, Brouwer et al. 1999). The composition of this seed bank is related to the recent history of the lake. In eutrophied lakes, many softwater species germinated in large amounts after mud removal, even if these species had not been observed for several decades. In acidified lakes, *Juncus bulbosus* was the dominant species in the seed bank and only a few other macrophyte species germinated, often in small quantities.

The aeration of the upper sediment layer improves after removal of anaerobic mud layers and temporal drainage of restored lakes. This strongly stimulates the germination of seeds from softwater macrophytes (Farmer & Spence 1987; Arts & van der Heijden 1990). In acidified lakes, germination and establishment could also have been stimulated by a somewhat elevated pH and better availability of nitrate and carbon dioxide in the first year after restoration, correlated with the desiccation and disturbance of the lake sediment. In both acidified and non-acidified lakes, *J. bulbosus* often became dominant in the first year after mud removal, but because the density of the vegetation was still low, this did not lead to the suppression of other macrophytes.

Further Development of Softwater Macrophytes

The further development of softwater macrophytes correlated strongly with the water quality. In eutrophied, and particularly in alkalized, lakes the nitrogen and phosphate availability in the water column decreased after sediment removal. This was also observed in many other lakes (Marsden 1989; Garnier et al. 1992). Recycling of nutrients from the sediment, as well as input of organic matter from the dense shore vegetation, was strongly reduced after mud removal. In alkalized lakes, the isolation from alkaline, nutrient-rich water contributed to the oligotrophication. This is indicated by the observed phosphate mobilization in Lake Beuven after incidental alkalization and by observations on Lake Banen (Brouwer et al. 1999). Furthermore, the carbon dioxide concentrations in the water column decreased strongly within 1 or 2 years, leading to a shift of species composition from J. bulbosus and other caulescent macrophytes to isoetid macrophytes. Thirteen years after restoration of Lake Beuven, the aquatic vegetation is still dominated by isoetids and the riparian zone is dominated by other softwater macrophytes. These results show that mud removal and isolation in eutrophied and/or alkalized softwater lakes can be an effective restoration measure, even in areas with very high nitrogen deposition.

However, renewed eutrophication occurred to a certain extent in the partially restored Lake Banen and Lake Broekse Wielen, but especially in many restored lakes not included in this study. Possible sources for renewed eutrophication are atmospheric deposition, influx of nitrogen-rich groundwater, diffusion from the sediment and unrestored parts, changes in hydrology and litter input.

In acidified lakes, the SRP concentrations remained low after restoration. Reduced phosphorus availability is frequently observed in acid lakes (Grahn et al. 1974; Kopáček et al. 2000). But growth conditions for softwater macrophytes in the water column soon became very

unfavorable. A low pH and the presence of ammonium as the dominant nitrogen source caused dieback of softwater macrophytes (Schuurkes et al. 1986; Maessen et al. 1992). When the water column contained enough carbon dioxide, fast growth of *J. bulbosus* and *Sphagnum* species contributed to this dieback. Several years after restoration, most softwater macrophytes disappeared again. Moreover, it is very likely that the seed bank of softwater macrophytes will be further reduced after mud removal and subsequent dieback of germinated softwater macrophytes.

Liming of acidified, ammonium-enriched lakes was tested in Lake Ven bij Schaijk (Bellemakers et al. 1996). Liming (in 3 subsequent years a total of 2850 kg/ha) was followed by reacidification to pH 4 within a year. J. bulbosus and several acid-resistant mosses remained the only macrophytes present. After mud removal and liming of Lake Scherpven, reacidification is more gradual. But, a high water turbidity and competition from Juncus effusus inhibited recolonization by softwater macrophytes. The expansion of *J. effusus* on sites where lime was supplied, and the higher SRP concentration in the sediment pore water, indicates local alkalization and internal eutrophication of the sediment. Increased coloration of the water column by humic acids and alkalization and eutrophication of the sediment is also reported from shallow parts of limed lakes in Scandinavia (Roelofs et al. 1994; Grøterud 1997). Therefore, liming is not considered as an appropriate measure to restore shallow, acidified softwater lakes in the Netherlands. Possibly, selective liming of the catchment area can serve as an alternative. Several authors mention a pH increase and an improved fish population during the 10 years following catchment liming in deeper lakes (Howells & Dalziel 1995; Driscoll et al. 1996; Traaen et al. 1997).

The supply of groundwater could be dosed more precisely, so alkalization of the sediment could be prevented. The carbon dioxide concentration in the water column returned to levels characteristic for softwater lakes, and ammonium is no longer the dominant nitrogen source. During the first years after restoration, nitrification of ammonium, proton exchange with the sediment and influx of ammonium-enriched, acid groundwater after periods of high rainfall caused a gradual decline to a pH between 4.5 and 5. Therefore, the difference in the water quality in acidified lakes where only the sediment was removed was not always significant (Fig. 3). It is expected that the water quality will stabilize when the base saturation in the sediment is restored and can act as a buffer against reacidification. Notwithstanding the fluctuations in water quality, a gradual recolonization by isoetid softwater macrophytes occurred in the four study lakes. On sites with a continuous influx of acidified, carbon dioxide-rich groundwater and on organic sediments, vegetation of other softwater macrophytes,

including *J. bulbosus*, developed. This is part of the natural vegetation pattern in such lakes.

Restoration of Softwater Lakes

Mud removal in softwater lakes is an effective restoration measure when a seed bank or a remnant population is present and an adequate water quality can be maintained. Therefore, it is essential to exclude all eutrophication sources. We conclude that adjusting the alkalinity of a dredged lake to its natural level is an effective method to control nitrogen and carbon cycles and to promote further expansion of softwater vegetation. Controlled supply of nutrient-poor alkaline water leads to a more complete restoration of soft waters and its vegetation than direct liming. In the near future, the groundwater supply can possibly be replaced by the supply of nutrient-poor, alkaline water from adjacent rivers. In many cases this may enable restoration of the historic situation.

Acknowledgments

This research has been supported by funding from the Dutch Ministry of Agriculture, Nature Conservation and Fisheries. The authors wish to thank Germa M. Verheggen for her assistance in the field and laboratory and the Limburg Water Pollution Control Authority for providing some additional data from Lake Banen. We received many useful comments during a special manuscript revision meeting. We thank all participants.

LITERATURE CITED

- Alhonen, P. 1985. Lake restoration: a sediment limnological approach. Aqua Fennica 15:269–273.
- Appelberg, M. 1998. Restructuring of fish assemblages in Swedish lakes following amelioration of acid stress through liming. Restoration Ecology 6:343–352.
- Arts, G. H. P., and R. A. J. M. van der Heijden. 1990. Germination ecology of *Littorella uniflora* (L.) Aschers. Aquatic Botany 37: 139–151.
- Arts, G. H. P., and R. S. E. W. Leuven. 1988. Floristic changes in shallow soft waters in relation to underlying environmental factors. Freshwater Biology **20**:97–111.
- Bellemakers, M. J. S., M. Maessen, G. M. Verheggen, and J. G. M. Roelofs. 1996. Effects of liming on shallow acidified moorland pools: a culture and a seed bank experiment. Aquatic Botany **54**:37–50.
- Brouwer, E., and J. G. M Roelofs. 1998. Groundwater as an alternative for the supply of eutrophied surface water in nutrient poor, acid-sensitive softwater pools. Mitteilungen der Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg 57:121–127.
- Brouwer, E., J. Soontiëns, R. Bobbink, and J. G. M. Roelofs. 1999. Sulphate and bicarbonate as key factors in sediment degradation and restoration of Lake Banen. Aquatic Conservation 9:121–132
- De Graaf, M. C. C., R. Bobbink, J. G. M. Roelofs, and P. J. M. Ver-

- beek, 1998. Differential effects of ammonium and nitrate on three heathland species. Plant Ecology **135**:185–196.
- Driscoll, C. T., C. P. Cirmo, T. J. Fahey, V. L. Blette, P. A. Bukaveckas, D. A. Burns, C. P. Gubala, D. J. Leopold, R. M. Newton, D. J. Raynal, C. L. Schofield, C. L. Yavitt, and D. B. Porcella. 1996. The experimental watershed liming study: comparison of lake and watershed neutralization strategies. Biogeochemistry 32:143–147.
- Farmer, A. M., and D. H. N. Spence. 1987. Flowering, germination and zonation of the submerged aquatic plant *Lobelia dort-manna* L. Journal of Ecology **75:**1065–1076.
- Garnier, J., A. Chestérikoff, P. Testard, and B. Garban. 1992. Oligotrophication after a nutrient reduction in a shallow sand-pit lake (Créteil Lake, Paris suburbs, France): a case of rapid restoration. Annales Limnologique 28:253–262.
- Grahn, O., H. Hultberg, and L. Landner. 1974. Oligotrophication – a self-accelerating process in lakes subjected to excessive supply of acid substances. Ambio 2:93–94.
- Grøterud, O. 1997. Humic colours in lakes in relation to acidification, hydraulic loading and liming. Verhandlungen der Internationale Vereinigung für theoretische und angewandte Limnologie **26:**313–318.
- Henriksen, A. 1965. An automated method for determining low-level concentrations of phosphate in fresh and saline waters. Analyst 90:29–34.
- Hindar, A., A. Henriksen, S. Sandøy, and A. J. Romundstad. 1998. Critical load concept to set restoration goals for liming acidified Norwegian waters. Restoration Ecology 6:353–363.
- Houdijk, A. L. F. M., and J. G. M. Roelofs. 1991. Deposition of acidifying and eutrophicating substances in Dutch forests. Acta Botanica Neerlandica 40:245–255.
- Howells, G., and T. Dalziel. 1995. A decade of studies at Loch Fleet, Galloway (Scotland): a catchment liming project and restoration of a brown trout fishery. Freshwater Forum 15:4–37.
- Hultberg, H., and I. B. Andersson. 1982. Liming of acidified lakes: induced long-term changes. Water, Air and Soil Pollution 18: 311–331
- Keeley, J. E. 1982. Distribution of diurnal acid metabolism in the genus *Isoetes*. American Journal of Botany **69**:254–257.
- Kempers, A. J., and A. Zweers. 1986. Ammonium determination in soil extracts by the salicylate method. Communications in Soil Science and Plant Analysis 17:715–723.
- Kopáček, J., J. Hejzlar, J. Borovec, P. Porcal, and I. Kotorová. 2000. Phosphorus inactivation by aluminium in the water column and sediments: lowering of in-lake phosphorus availability in an acidified watershed-lake ecosystem. Limnology and Oceanography 45:212–225.
- Lucassen, E. C. H. E. T., R. Bobbink, M. M. A. Oonk, T. E. Brandrud, and J. G. M. Roelofs. 1999. The effects of liming and reacidification on the growth of *Juncus bulbosus*: a mesocosm experiment. Aquatic Botany 64:95–103.
- Maberly, S. C. 1985. Photosynthesis by *Fontinalis antipyretica*. I. Interaction between photon irradiance, concentration of carbon dioxide and temperature. New Phytologist **100**:127–140.
- Madsen, T. V. 1985. A community of submerged aquatic CAM plants in lake Kalgaard, Denmark. Aquatic Botany 23:97– 108.
- Maessen, M., J. G. M. Roelofs, M. J. S. Bellemakers, and G. M. Verheggen. 1992. The effects of aluminium, aluminium/calcium ratios and pH on aquatic plants from poorly buffered environments. Aquatic Botany 43:115–127.
- Marsden, M. W. 1989. Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. Freshwater Biology 21:139–162.
- Nilssen, J. P. 1980. Acidification of a small watershed in southern Norway and some characteristics of acidic aquatic environ-

- ments. Internationale Revue der gesamten Hydrobiologie **65**: 163–201.
- Risgaard-Petersen, N., and K. Jensen. 1997. Nitrification and denitrification in the rhizosphere of the aquatic macrophyte *Lobelia dortmanna* L. Limnology and Oceanography **42:**529–537.
- Roelofs, J. G. M. 1983. Impact of acidification and eutrophication on macrophyte communities in soft waters in the Netherlands. I. Field observations. Aquatic Botany 17:139–155.
- Roelofs, J. G. M., R. Bobbink, E. Brouwer, and M. C. C. de Graaf. 1996. Restoration ecology of aquatic and terrestrial vegetation on non-calcareous sandy soils in The Netherlands. Acta Botanica Neerlandica 45:517–541.
- Roelofs, J. G. M., T. E. Brandrud, and A. J. P. Smolders. 1994. Massive expansion of *Juncus bulbosus* L. after liming of acidified SW Norwegian lakes. Aquatic Botany 48:187–202.
- Roelofs, J. G. M., J. A. A. R. Schuurkes, and A. J. M. Smits. 1984. Impact of acidification and eutrophication on macrophyte communities in soft waters. II. Experimental studies. Aquatic Botany 18:389–411.
- Rudd, J. W. M., C. A. Kelly, D. W. Schindler, and M. A. Turner. 1988. Disruption of the nitrogen cycle in acidified lakes. Science 140:1515–1517.
- Salsac, L., S. Chaillou, J.-F. Morot-Gaudry, C. Lesaint and E. Jolivet. 1987. Nitrate and ammonium nutrition in plants. Plant Physiology and Biochemistry 25:805–812.
- Sand-Jensen, K. 1983. Photosynthetic carbon sources of stream macrophytes. Journal of Experimental Botany 34:198–210.
- Schindler, D. W., 1974. Eutrophication and Recovery in Experimental Lakes: Implications for Lake Management. Science 184:897–899.
- Smolders, A. J. P. 1995. Mechanisms involved in the decline of aquatic macrophytes; in particular of *Stratiotes aloides* L. M.Sc. Thesis. University of Nijmegen, The Netherlands.
- Smolders, A., and J. G. M. Roelofs. 1995. Internal eutrophication,

- iron limitation and sulphide accumulation due to the inlet of river Rhine water in peaty shallow waters in The Netherlands. Archiv für Hydrobiologie **133**:349–365.
- Smolders, A. J. P., C. Den Hartog, C. B. L. van Gestel, and J. G. M. Roelofs. 1996. The effects of ammonium on growth, accumulation of free amino acids and nutritional status of young phosphorus deficient *Stratiotes aloides* plants. Aquatic Botany 53:85–96.
- Schuurkes, J. A. A. R., C. J. Kok, and C. Den Hartog. 1986. Ammonium and nitrate uptake by aquatic plants from poorly buffered and acidified waters. Aquatic Botany 24:131–146.
- Technicon. 1969. Technicon auto analyzer methodology, industrial method 11 and 33–69W. Technicon Corporation, New York.
- Traaen, T. S., T. Frogner, A. Hindar, E. Kleiven, A. Lande, and R. F. Wright. 1997. Whole-catchment liming at Tjønnstrond, Norway: an 11-year record. Water, Air and Soil Pollution 94: 163–180.
- van Dam, H., and R. F. M. Buskens. 1993. Ecology and management of moorland pools: balancing acidification and eutrophication. Hydrobiologia 265:225–263.
- Wetzel, R. G., E. S. Brammer, K. Lindström, and C. Forsberg, 1985. Photosynthesis of submersed macrophytes in acidified lakes. II. Carbon limitation and utilization of benthic CO₂ sources. Aquatic Botany 22:107–120.
- Wigand, C., F. O. Andersen, K. K. Christensen, M. Holmer, and H. S. Jensen, 1998. Endomycorrhizae of isoetids along a biogeochemical gradient. Limnology and Oceanography 43: 508–515.
- Wium-Andersen, S. 1971. Photosynthetic uptake of free CO₂ by roots of *Lobelia dortmanna*. Physiologia Plantarum **25**:245–248.
- Wium-Andersen, S., and J. M. Andersen. 1972. The influence of vegetation on the redox profile of the sediment of Grane Langsø, a Danish Lobelia lake. Limnology and Oceanography 17:943–947.