Catchment Liming to Restore Degraded, Acidified Heathlands and Moorland Pools

Edu Dorland, ¹ Leon J. L. van den Berg, ² Emiel Brouwer, ³ Jan G. M. Roelofs, ² and Roland Bobbink ^{1,4}

Abstract

Current restoration measures of degraded, acidified heathland ecosystems have not always been successful in the Netherlands. Positive effects of a restored hydrology are often counteracted by acidification of the soil and the local groundwater system. Liming of the heathlands in the catchment of moorland pools might contribute to the restoration of both habitats. Experimental catchment liming was carried out in two degraded Dutch heathlands, with doses varying between 2 and 6 tons/ha. Catchment liming resulted in increased pH and base cation concentrations in the highest elevated limed parts, as well as in the lower situated, nonlimed heath areas and moorland pools. Generally, catchment liming created suitable con-

ditions for the return of heathland target species, and the positive effects lasted for at least 6 years. The response of the heathland vegetation to the liming has, however, been slow because only a small number of endangered plant species increased in abundance. In contrast, four Red List soft-water macrophytes strongly increased in abundance in the moorland pool. Our results show that, even with the slow return of Red List plant species, catchment liming can be a successful management tool for the restoration of the acidified heathland landscape.

Key words: calcium, catchment liming, heathlands, moorland pools, Red List plant species, restoration.

Introduction

Heathlands have, for a long time, been a prominent part of the West European landscape. They contain plant communities where the dominant life-form is that of the small-leaved dwarf shrubs (especially Ericaceae species) forming a canopy of 1 m or less above soil surface. Ericoid heathlands are widespread in the Atlantic and sub-Atlantic parts of Europe. In these parts of the European continent, natural heathlands are restricted to a narrow coastal zone. Inland lowland heaths are seminatural, although they have existed for several centuries. Most dry heathland communities are found on nutrient-poor mineral soils with a low pH (3.5–4.5). The vegetation is relatively species poor but with several characteristic species (Gimingham et al. 1979; Ellenberg 1988).

A small part (5–10%) of the West European heathland landscape is covered with lowland heath of wet habitats, dominated by *Erica tetralix*. These wet-heath communities (*Ericion tetralicis*) are generally more species-rich than those of dry habitats. Hot spots of species richness have been especially prominent in situations where relatively base-rich soils (loam or boulder clay) are surfacing in wet

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situations or in discharge areas of local hydrological systems. These species-rich wet heaths have clearly higher soil pH (4.5–6.0) and are thus weakly buffered via cation exchange processes. However, it is likely that many typical wet heaths formerly had soil pH around 4.5–5.0 because of the seasonal water logging that increased soil pH by redox processes and because of the lack of acidifying atmospheric inputs. This is clearly suggested by the much higher frequencies of plant species of weakly buffered soils in vegetation descriptions from before the increase of atmospheric acidification (De Smidt 1975; Roelofs et al. 1996).

During the last century, the distribution of wet heath-lands in West Europe has decreased strongly (de Smidt 1975, 1979; Aerts & Heil 1993; Webb 1998) and a considerable part is nowadays situated in the Netherlands. Throughout Western Europe the plant species diversity of wet heaths has decreased as a consequence of acidification, eutrophication, and drainage (Houdijk et al. 1993; Roelofs et al. 1996; Bobbink et al. 1998b). Because of the decreased distribution and species diversity, heathlands are internationally regarded as highly valuable ecosystems (Gimingham 1992; Webb 1998), and restoration of these habitats is important.

Although some restoration projects have resulted in the recovery of the former species-rich heath vegetation (e.g., Jansen et al. 1996; Roelofs et al. 1996), the results of many restoration efforts have often been disappointing. In particular, the acidification of formerly weakly buffered heathlands could not easily be restored, and the

 ¹ Section of Landscape Ecology, Department of Geobiology, Utrecht University, P.O. Box 800.84, 3508 TB Utrecht, The Netherlands.
 ² Department of Aquatic Ecology & Environmental Biology, Radboud University Nijmegen, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands.

³ Research center B-WARE B.V., Radboud University Nijmegen,

Toernooiveld 1, 6525 ED Nijmegen, The Netherlands.

Address correspondence to R. Bobbink, email R.Bobbink@bio.uu.nl

endangered, acid-sensitive species did not return (Roelofs et al. 1996; Bobbink et al. 1998a). Present restoration measures of heathland ecosystems in the Netherlands are sod cutting (i.e., the removal of accumulated organic matter including the vegetation) and, in wet heathlands, restoration of the original hydrology. Sod cutting is very effective in removing excess nutrients from eutrophicated heathlands (Bakker 1989; Mitchell et al. 2000) but does not counteract soil acidification (Dorland et al. 2003; Van den Berg et al. 2003). In addition, removal of organic matter containing nitrifying bacteria results in the accumulation of ammonium (NH₄⁺) in the soil (Dorland et al. 2004). Within 1–2 years of removal of organic matter, the NH₄⁺ concentrations may reach values that are known to be toxic to many Red List, acid-sensitive heathland species (de Graaf et al. 1998; Dorland et al. 2003).

In wet heathlands, the deleterious effects of drainage can be reversed, for example, by blocking drainage ditches to increase the influence of (local) groundwater (Roelofs et al. 1996). If local groundwater has been acidified, however, the success of hydrological restoration will be small (e.g., Gunn et al. 2001). In such cases, deacidification of groundwater should be an additional target for restoration measures.

Liming is a widely used method to counteract the loss of biodiversity due to acidification. Since the 1970s, limestone has been applied directly to acidified lakes, rivers, and forests (e.g., Henrikson et al. 1995; Eggleton et al. 1996; Appelberg & Svenson 2001), resulting in improved soil and water chemistry. However, negative effects of liming have also been reported. The application of high doses of lime to Norwegian and Swedish lakes has resulted in the accumulation of CaCO₃ in the littoral sediments. Consequently, mineralization rates of the alkalinized sediments increased, causing eutrophication of the lakes. After reacidification of these lakes, carbon dioxide (CO₂) levels and NH₄⁺ and phosphate (PO₄³⁻) concentrations strongly increased in the sediment pore water (Roelofs et al. 1994; Brandrud 2002). This resulted in a massive expansion of Bulbous rush (Juncus bulbosus) and the concomitant decrease of typical soft-water macrophytes (Roelofs et al. 1994).

Alkalinization of the sediment and subsequent degradation of the vegetation does not occur when lime is applied to the catchment of lakes or rivers (Brouwer et al. 2002; Roelofs et al. 2002). The added Ca²⁺ and bicarbonate (HCO₃⁻) are slowly released from the limed soil and cause a long-term increase of the buffering capacity of the water and soil in the catchment area. These buffering compounds will be transported by run-off and subsurface groundwater flow toward the acidified surface waters. The pH and base cation concentrations will thus be increased along the whole height gradient. However, some studies have reported increased leaching of nitrate (NO₃⁻) after liming of forest soils, resulting from increased decomposition (e.g., Traaen et al. 1997). Sod cutting or other measures to remove nutrients from the topsoil of the catchments prior to liming might minimize these risks. The sustainability of the positive effects of catchment liming may be quite long because of the continuous leaching of base-rich compounds from limed soils (Hornung 1995; Traaen et al. 1997). Catchment liming has successfully been applied in studies in acidified lakes and streams in Scandinavia, Britain, Canada, and in the United States (Hornung 1995; Nystrom et al. 1995; Porcella et al. 1995; Rundle et al. 1995; Traaen et al. 1997; Hindar et al. 2003). In these studies, little attention was paid to the restoration of degraded terrestrial ecosystems on which the lime was applied.

The aim of our study is to determine whether catchment liming after sod cutting is an effective method to counteract both the acidification and the accumulation of $\mathrm{NH_4}^+$ in wet and dry heathlands and adjacent moorland pools simultaneously. Furthermore, we investigated if catchment liming could successfully restore the characteristic vegetation of these ecosystems.

Methods

Site Descriptions

In the Netherlands, two acidified and eutrophicated heathlands, of which the local hydrology was well known, were selected for catchment liming. One site was in the nature reserve, Schaopedobbe, situated in the north of the Netherlands (lat 52°57′N, long 6°15′E). In this area, sandy soils of Pleistocene origin surround a formerly weakly buffered moorland pool. Wet-heath vegetation and matgrass swards cover the pool margin, whereas a dry heath vegetation has developed on the higher edges. The second study area was located in the nature reserve, the Bieze, situated in the center of the Netherlands (lat 52°14'N, long 5°48'E). The Bieze consists of a complex of wet and dry heaths surrounding several small, and one larger, weakly buffered moorland pools. The soil of the Bieze consists of fine to coarse sand with loam. Both areas had been sod cut in 1990, which reduces the risk of enhanced mineralization of soil organic matter following liming.

In both areas, two transects were laid out along a height gradient (Fig. 1). These transects each contained three terrestrial sampling points (High, Middle, and Low) and one sampling point in the moorland pool. The vegetation of the High, Middle, and Low sampling points could be characterized as dry, moist, and wet heath, respectively. The addition of lime in Schaopedobbe and the Bieze was carried out on 20 November and 16 December 1997, respectively. Catchment liming was restricted to the highest elevated zone at Schaopedobbe, whereas in the Bieze, the High and Middle zones were limed. Dolokal was used in both study areas at rates ranging from 2.3 to 6.3 tons/ha (Fig. 1).

Soil, Water, and Vegetation Analyses

Four samples of the upper 10 cm of the soil (2.5-cm-diameter auger) were collected in Schaopedobbe prior to and directly after liming in 1997 and once a year from

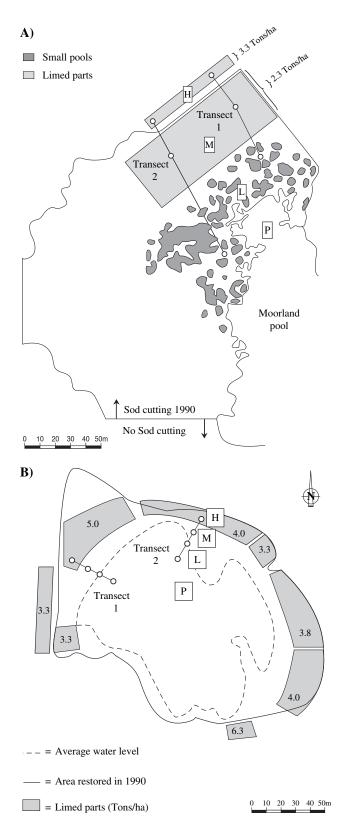


Figure 1. Schematic view of the Bieze (A) and Schaopedobbe (B). In each study area, two transects were laid out. Limed areas indicated by rectangles with doses in tons per hectare. The limed areas had been sod cut in 1990. Relative heights of sampling points are indicated as H = High, M = Middle, L = Low, and P = moorland pool.

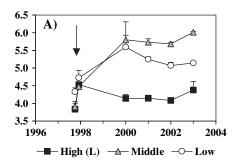
2000 to 2003 at each of the three terrestrial sampling points. In the Bieze, soil sampling started 1 week after catchment liming in 1997. Soil data collected in November 1996 from this area were used for the pre-treatment situation. The soil samples were transported to the laboratory in a cool box, stored at 4°C, and processed within 2 days. After homogenizing the four samples from each plot, 35 g of fresh soil was extracted with 100 ml 0.2 M NaCl or demineralized water on a rotary shaker (100 rpm) for 1 hour. After measuring the soil pH (SenTix 41 electrode), the samples were centrifuged at 4,000 rpm for 5 minutes. Supernatants were filtered through a Whatman GF/C filter and stored at -20°C until further analysis. Soil moisture content was measured after drying 15 g of fresh soil at 105°C for 24 hours. Water-extractable concentrations of Al3+, K+, NO3-, and PO43-, and 0.2 M NaCl-exchangeable concentrations of Ca²⁺, Mg²⁺, and NH₄⁺ were analyzed colorimetrically using a Skalar continuous flow analyzer (Skalar 40, Skalar Analytical BV, Breda, The Netherlands).

Surface water samples from the moorland pools were collected yearly beginning 1994 in the spring and at the end of each summer. Alkalinity was determined by titration of 100 ml sample with 0.01 M HCl down to pH 4.2 using a radiometer Copenhagen type TIM800 in combination with an ABU901 Autoburette (Radiometer Copenhagen) and an ORION pH electrode model 91-56. Citric acid (0.25 g/L) was added to the samples to prevent metal ions from precipitating, and samples were stored at -20°C until further analysis. Nutrient concentrations were measured on an inductively coupled plasmaspectrophotometer (Spectroflame Flame VML2, Spectro AI, Kleve, Germany).

Each summer from 2000 to 2003, vegetation relevées were made at all terrestrial sampling points. Two plots of 1.5×1.5 m were laid out on both sides of each sampling point. The number and cover percentage of all plant species were determined visually within these plots according to the Braun-Blanquet approach (Westhoff & Van der Maarel 1978). The plant species were divided into three classes: Red List target species (Bal et al. 2003), species characteristic for heathlands (Schaminée et al. 1995), and nontarget species. The effects of catchment liming on the aquatic vegetation in the moorland pools at each site was determined by monitoring the distribution of the four soft-water macrophytes present before and after catchment liming. The distribution of Floating club-rush (Eleogiton fluitans), Bog pondweed (Potamogeton polygonifolius), and Ranunculus ololeucos in the moorland pools of the Bieze and of Floating water plantain (Luronium natans) in Schaopedobbe was mapped in 1994 and 2003. All four species are on the Dutch Red List and internationally endangered (Van der Meijden 2002).

Statistical Analyses

Statistical tests were carried out using the Statistical Program for the Social Sciences 10.0 (SPSS, Inc. 1989–1999).



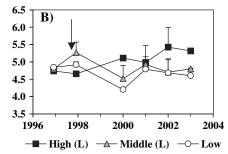


Figure 2. Soil pH- (H_2O) (+SE) along the height gradient from High to Low sampling points at Schaopedobbe (A) and the Bieze (B) before and after catchment liming. When and in which zone lime was applied is indicated by the arrow and (L), respectively.

All data were tested for normality using the Kolmogorov-Smirnov tests. One-way analysis of variance tests were carried out to test for the differences between the zones of each study area. If necessary, data were logarithmically transformed to stabilize variances between groups. Non-parametric Mann–Whitney U tests were performed, if transformations of the data were unsuccessful. Differences in mean values of the years before and after catchment liming were tested with Student t tests. To test for significant correlations between number of plant species and years since start of the study, Pearson's correlation coefficients were calculated. The significance level, α , was 0.05 in all tests.

Results

pH-(H₂O)

Catchment liming at Schaopedobbe resulted in a measurable but insignificant increase in pH-(H₂O) along the whole height gradient from the highest elevated limed parts to the lowest elevated nonlimed parts (Fig. 2A). From 1998 to 2003, soil pH at the Middle and Low sampling points increased to a level between 5.0 and 6.0, which was in the range characteristic for weakly buffered soil conditions. In contrast, pH at the High sampling points increased to 4.5 in 1997 but subsequently decreased to a level of about 4.1. Six years after the application of lime, the pH of all the sampling points was still higher than it had been before liming, but the difference was significant for the Middle sampling points only. In the Bieze, long-term positive trends of liming on soil pH were found in the highest part only (Fig. 2B).

In both study areas, the pH of the moorland pools increased after catchment liming (Fig. 3). Although pH decreased since 1999 at Schaopedobbe, the mean pH of the years after liming (1998–2002) was significantly higher compared to those before liming (1994–1997). In the Bieze, pH was significantly higher following liming as well (4.26 and 4.86 before and after liming, respectively), and no subsequent decrease was observed.

Base Cations

At Schaopedobbe and the Bieze, the concentrations of the most important base cations $(Ca^{2+}, Mg^{2+}, and K^+)$ strongly increased following catchment liming (Fig. 4A & 4B). These effects were found along the height gradients, similar to the pH effects. In particular, Ca^{2+} , and to a lesser extent Mg^{2+} , contributed to this increase. At Schaopedobbe, the greatest increase was found in the nonlimed Middle part. In the upper and middle zones of both areas, base cation concentrations fluctuated since 2000, whereas in the lower part the concentrations stabilized.

The alkalinity of the moorland pools greatly increased following catchment liming (Fig. 5). In both areas, these effects were observed within 1 year after the addition of lime. Mean alkalinity in the years after liming was significantly higher, compared to preliming years (220.8 versus 31.6 and 50.4 versus 13.7 μeq/L of Schaopedobbe and the Bieze, respectively).

Nutrients

Gradually increasing concentrations of NH₄⁺ and NO₃⁻ were found in the limed High parts of Schaopedobbe (Fig. 6). Maximum concentrations of NH₄⁺ were reached in 2002, 5 years after the lime application. In the Bieze and in Middle and Low parts of Schaopedobbe, no

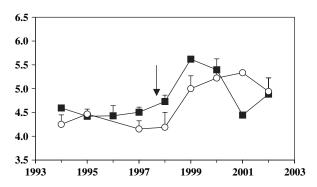


Figure 3. Mean annual values of pool water pH (+SE) at Schaopedobbe (filled squares) and at the Bieze (open circles) from 1994 to 2002. The arrow indicates when lime was applied.

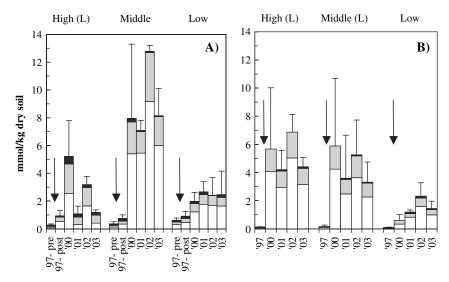


Figure 4. Mean 0.2 M NaCl-exchangeable soil base cation concentrations (+SE; Ca^{2+} = white, Mg^{2+} = gray, and K^+ = black) along the height gradient from High to Low sampling points at Schaopedobbe (A) and the Bieze (B) before and after catchment liming in 1997. When and in which zone lime was applied is indicated by the arrow and (L), respectively.

significantly increased NH₄⁺ and NO₃⁻ concentrations were found after liming.

In the moorland pools at Schaopedobbe and Bieze, NH₄⁺ and NO₃⁻ concentrations were high in 1995 and decreased in subsequent years (Fig. 7). No significant changes in these concentrations, or in the NH₄⁺:NO₃⁻ ratio (data not shown), occurred in both areas following catchment liming.

At the Bieze, Al:Ca ratios, which are indicative for possible toxic effects of dissolved Al³⁺ concentration, ranged between 14 and 16 before catchment liming and had significantly decreased 5 years after catchment liming (Fig. 8A). In Schaopedobbe, Al:Ca ratios before catchment liming were lower compared to the Bieze and decreased following catchment liming as well (Fig. 8B). These differences were not significant, however.

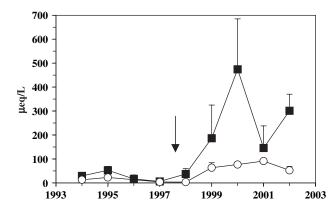


Figure 5. Mean annual values of pool water alkalinity (+SE) at Schaopedobbe (filled squares) and at the Bieze (open circles) from 1994 to 2002. The arrow indicates when lime was applied.

Vegetation

Catchment liming improved the abiotic conditions of heathlands and moorland pools. However, only small positive trends in the number of Red List and characteristic plants species of wet heaths were observed, and no significant differences between years were found at Schaopedobbe during the study period 2000–2003 (Fig. 9A). There was no significant positive correlation between the number of plant species and years since liming. In the Bieze, no positive trend in number of species over time was found (Fig. 9B). Among the target species that returned or increased in abundance in both study areas were Marsh gentian (Gentiana pneumonanthe), Marsh clubmoss (Lycopodiella inundata), White beak-sedge (Rhynchospora alba), Brown beak-sedge (R. fusca), Oblong-leaved sundew (Drosera intermedia), and Round-leaved sundew (D. rotundifolia), all Dutch Red List species.

The distribution of *Eleogiton fluitans*, *Potamogeton polygonifolius*, and *Ranunculus ololeucos* in the moorland pools of the Bieze increased considerably following catchment liming (Fig. 10). The number of pools in which these species covered more than 25% increased from 4 pools in 1994 to 14 in 2003. During this period, the distribution of *Luronium natans* increased approximately 10-fold following catchment liming in Schaopedobbe. In addition, the abundant growth of *Juncus bulbosus* and several acidtolerant *Sphagnum* species, which occurred before catchment liming in many pools in the Bieze, disappeared following the lime application (data not shown).

Discussion

Our results showed that the application of Dolokal on the catchments of two acidified heathlands resulted in the

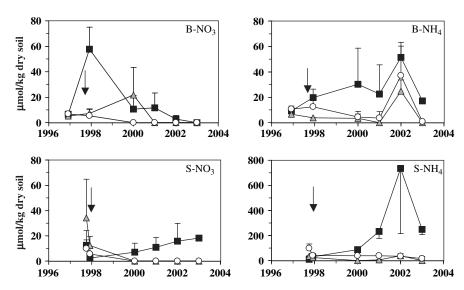


Figure 6. Soil water-extractable NO_3^- concentrations and 0.2 M NaCl-exchangeable NH_4^+ concentrations (+SE) along the height gradient at the Bieze (B; upper graphs) and Schaopedobbe (S; lower graphs) before and after catchment liming. Black squares = High, gray triangles = Middle, and open circles = Low sampling points. Arrows indicate when lime was applied. Note the different y-axis of the S- NH_4^+ graph.

successful restoration of abiotic conditions in the highest elevated limed parts, as well as in the lower situated, nonlimed heath areas and moorland pools, hence along the whole height gradient. Increased pH, Ca²⁺ concentrations, and alkalinity and decreased Al3+ concentrations following catchment liming have also been reported for streams and lakes (e.g., Porcella et al. 1995; Rundle et al. 1995; Menendez et al. 1996; Simmons & Cieslewicz 1996; Traaen et al. 1997; Hindar et al. 2003). The dissolution rate of Ca²⁺ from the applied lime will depend on the acidity of rain water and the type of lime. Kreutzer (1995) found that 50% of the applied dolomite had dissolved during the first year and the rate decreased exponentially to 90% after 4 years. During the first 4 years of the study of Alenäs et al. (1991), 73% had dissolved from the di-Ca-silicate slag applied. As a result, the input of Ca²⁺ and HCO₃⁻ ions into the soil and soil water is high, hence restoring the cation exchange capacity (CEC). The subsequent transport of mobile Ca²⁺ and HCO₃⁻ ions toward the lower parts of the wet heathlands and the moorland pools by groundwater flows may be slow depending on the

hydrological gradient and the permeability of the soil. Consequently, catchment liming will result in a low but continuous input of Ca²⁺ and HCO₃⁻ ions into topographically lower areas, causing positive effects on soil and pool water chemistry. In Schaopedobbe, a rapid transport of Ca²⁺ ions by run-off or subsurface water flows following catchment liming was found because increased base cation concentrations were found in the lower situated nonlimed parts within 1 month.

The positive effects of catchment liming on soil and water chemistry can be extended over several years. In our study, increased pH and base cation concentrations persisted throughout the study period, thus lasting for at least 6 years. Similar results were found for limed streams in Wales (5 years; Rundle et al. 1995) and Norway (7 years; Hindar et al. 2003) and for Swedish lakes (>8 years; Fransman & Nihlgård 1995). Others observed persistence of mitigating effects of catchment liming for more than 10 years (Hornung 1995; Traaen et al. 1997). The persistence might be even more prolonged if the input of acidifying compounds by atmospheric deposition continues to

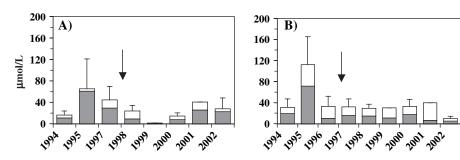
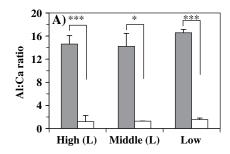


Figure 7. Pool water NO₃⁻ (white) and NH₄⁺ (gray) concentrations (+SE) at the Bieze (A) and Schaopedobbe (B) from 1994 to 2002. Arrows indicate when lime was applied.



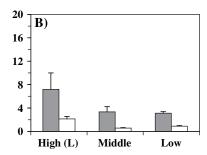


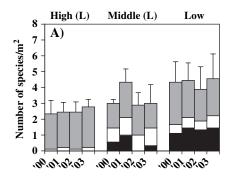
Figure 8. Soil water-extractable Al:Ca ratios (+SE) at the Bieze (A) and Schaopedobbe (B) before (gray) and 5 years after (white) catchment liming. Significant differences between years are indicated by asterisks (*p < 0.05, **p < 0.01, ***p < 0.001). (L) indicates the zone in which lime has been applied.

decrease, as is the case in recent decades (Eerens et al. 2001). Studies in which no ameliorative effects of catchment liming on surface waters were found are also known, however. Lorz et al. (2003) repeatedly limed a forest catchment in the Ore Mountains (Germany) over a period of 7 years and found only a small increase in pH and decreasing concentrations of Ca²⁺ and Mg²⁺. Possibly, groundwater discharge from humic forest soils is more difficult to ameliorate due to their high (potential) CEC, whereas sod-cut heathland soils are predominantly mineral.

Besides the positive effects of catchment liming on soil chemistry, some negative effects have also been documented. Increased loss of NO_3^- via run-off was found in the studies of Traaen et al. (1997). This increase may persist for a period of 1–2 years and may be caused by increased mineralization of soil organic matter, and hence nitrification, due to the higher soil pH. In our study, no increased NO_3^- concentrations were found. However, catchment liming did increase NH_4^+ concentrations in Schaopedobbe. In 2002, 5 years after liming, NH_4^+ concentrations had reached values up to 750 μ mol/kg dry soil. This result contradicts our presumption that sod cutting prior to catchment liming would prevent increased mineralization. The period of 7 years between sod cutting and catchment liming might have been too long to forestall

these negative effects because a new organic layer will have accumulated during these years. Sod cutting directly before liming seems to be necessary to prevent enhanced mineralization. The maximum NH₄⁺ concentrations found in Schaopedobbe might be toxic for many Red List heathland plants as found in previous research (De Graaf et al. 1998; Dorland et al. 2003). Because these effects occurred only in the high parts, vegetated by a species-poor dry heath vegetation, we observed no negative effects on the vegetation. In the Bieze, increased values were found in all terrestrial sampling points, but these values did not reach toxic concentrations. The higher increase in NH₄⁺ concentrations following liming compared to the increase in NO₃ concentrations indicates that nitrification is still limited due to low soil pH. At the time of maximum NH₄⁺ concentration in Schaopedobbe, mean soil pH was about 4.1. Roelofs et al. (1985) found that nitrification is seriously hampered below soil pH values of 4.1–4.4.

In our study, no negative effects of catchment liming on plant species composition were found, although damage to the (terrestrial) vegetation is sometimes said to be the major negative effect of catchment liming (Henrikson et al. 1995; Traaen et al. 1997). Liming of Swedish bogs, for example, resulted in death of *Sphagnum* mosses (Henrikson et al. 1995). In our study, the number of (Red List) phanerophyte plant species showed a positive trend



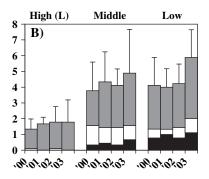


Figure 9. Plant species diversity of terrestrial zones at the Bieze (A) and Schaopedobbe (B) from 2000 to 2003. Red List species are indicated in black, characteristic species for heathland ecosystems are indicated in white, and other species are presented in gray. (L) indicates the zone in which lime has been applied in 1997.

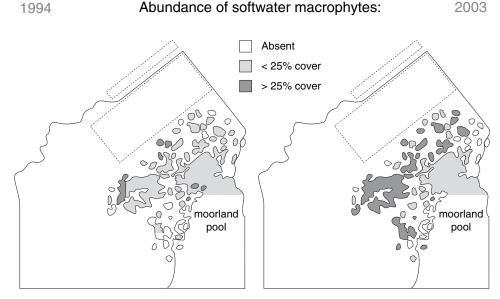


Figure 10. Expansion of *Eleogiton fluitans*, *Potamogeton polygonifolius*, and *Ranunculus ololeucos* in pools at the Bieze from 1994 (A) to 2003 (B). Dark gray areas, >25% cover; light gray areas, <25% cover; and white areas, absent.

in Schaopedobbe and remained constant in the Bieze. Vigorous growth of Juncus bulbosus and Sphagnum species ceased in the pools of the Bieze, and Red List species, such as Eleogiton fluitans and Potamogeton polygonifolius, expanded strongly. This change may be explained by the increased pH and alkalinity of the moorland pools. As pH increases, a shift occurs from CO2 as the inorganic carbon form at low pH toward HCO₃ at higher pH (Hagley et al. 1996). Plant species that depend on high CO₂ and NH₄⁺ concentrations for their growth, such as *J. bulbosus* (Roelofs et al. 1995; Lucassen et al. 1999), will be replaced by soft-water macrophytes (Brouwer & Roelofs 2002; Roelofs et al. 2002). Brandrud (2002) also reported that in the years following lake liming, acid-sensitive species increased in abundance. These species were mainly elodeids, such as Alternate water-milfoil (Myriophyllum alterniflorum) and Red pondweed (P. alpinus), and nymphaeids such as P. polygonifolius and Broad-leaved pondweed (P. natans).

The response of the terrestrial vegetation to improved abiotic conditions was relatively small in both study areas, though some Red List species returned or increased in abundance. Most of them were characteristic for early successional stages, such as both *Drosera* and *Rhynchospora* species and *Lycopodiella inundata*. The return of other Red List species may be limited by low seed availability. Many Red List species of later successional stages produce short-lived seeds (Thompson et al. 1997; Bekker et al. 1998) and will be absent in the seed bank of degraded wet heaths, as was shown in seed bank analyses of two other wet heathlands (Dorland 2004). When remnant populations of these species are not present at nearby sites, the establishment of these species may be hampered seriously. The chance of long-distance seed dispersal of many Red

List plant species has been shown to be very low in the fragmented Dutch landscape (Soons & Heil 2002).

In conclusion, catchment liming has proven to be a moderate to long-term stable method to ameliorate the chemistry of acidified heathland soils and moorland pools. Abiotic variables, like pH, buffering capacity, and Al^{3+} concentrations, were successfully improved. Acidification was successfully counteracted, but some mobilization of NH_4^+ occurred. This can probably be prevented by sod cutting immediately prior to liming. Typical soft-water macrophytes strongly expanded after catchment liming. The terrestrial vegetation, however, showed only a weak response. This might be a consequence of the mobilization of NH_4^+ and a lack of viable seeds or poor seed dispersal of the Red List plant species to the amended sites.

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LITERATURE CITED

Aerts, R., and G. W. Heil. 1993. Heathland: patterns and processes in a changing environment. Kluwer Academic Publishers, Dordrecht, The Netherlands.

- Alenäs, I., B. I. Andersson, H. Hultberg, and A. Rosemarin. 1991. Liming and reacidification reactions of a forest lake ecosystem, lake Lysevatten, in SW Sweden. Water, Air and Soil Pollution 59:55–77.
- Appelberg, M., and T. Svenson. 2001. Long-term ecological effects of liming—the ISELAW programme. Water, Air and Soil Pollution 130:1745–1750.
- Bakker, J. P. 1989. Nature management by grazing and cutting. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Bal, D., H. M. Beije, M. Fellinger, R. Haveman, and A. J. F. M. van Opstal. 2003. Handboek Natuurdoeltypen, Expertisecentrum LNV. Ministry of Agriculture, Nature and Food quality, Wageningen, The Netherlands.
- Bekker, R. M., J. H. J. Schaminée, J. P. Bakker, and K. Thompson. 1998. Seed bank characteristics of Dutch plant communities. Acta Botanica Neerlandica 47:15–26.
- Bobbink, R., M. C. C. De Graaf, G. M. Verheggen, and J. G. M. Roelofs. 1998a. Do heathland habitats have a future in the Netherlands? (In Dutch) Pages 131–159 in R. Bobbink, J. G. M. Roelofs, and H. B. M. Tomassen, editors. Effectgerichte maatregelen en behoud biodiversiteit in Nederland. University of Nijmegen, Nijmegen, The Netherlands.
- Bobbink, R., M. Hornung, and J. G. M. Roelofs. 1998b. The effects of air borne nitrogen pollutants on species diversity in natural and seminatural European vegetation. Journal of Ecology 86:717–738.
- Brandrud, T. E. 2002. Effects of liming on aquatic macrophytes, with emphasis on Scandinavia. Aquatic Botany 73:395–404.
- Brouwer, E., R. Bobbink, and J. G. M. Roelofs. 2002. Restoration of aquatic macrophyte vegetation in acidified and eutrophied softwater lakes: an overview. Aquatic Botany **73**:405–431.
- Brouwer, E., and J. G. M. Roelofs. 2002. Oligotrophication of acidified, nitrogen-saturated softwater lakes after dredging and controlled supply of alkaline water. Archiv für Hydrobiologie 155:83–97.
- de Graaf, M. C. C., R. Bobbink, J. G. M. Roelofs, and P. J. M. Verbeek. 1998. Differential effects of ammonium and nitrate on 3 heathland species. Plant Ecology 135:185–196.
- de Smidt, J. T. 1975. Heathland vegetations of the Netherlands. Ph.D. dissertation. Utrecht University, Utrecht, The Netherlands.
- de Smidt, J. T. 1979. Origin and destruction of Northwest European heath vegetation. Pages 411–435 in O. Wilmanns and R. Tüxen, editors. Werden und Vergehen von Pflanzengesellschaften. J. Cramer, Vaduz, Liechtenstein.
- Dorland, E. 2004. Ecological restoration of wet heaths and matgrass swards. Bottlenecks and solutions. Ph.D. dissertation. Utrecht University, Utrecht, The Netherlands.
- Dorland, E., R. Bobbink, J. H. Messelink, and J. T. A. Verhoeven. 2003. Soil ammonium accumulation after sod cutting hampers the restoration of degraded wet heathlands. Journal of Applied Ecology 40:804–814
- Dorland, E., L. J. L. van den Berg, A. J. van den Berg, M. Vermeer, J. G. M. Roelofs, and R. Bobbink. 2004. The effects of sod cutting and additional liming on potential net nitrification in heathland soils. Plant and Soil 265:267–277.
- Eerens, H. C., J. D. van Dam, J. P. Beck, J. H. J. Dolmans, W. A. J. van Pul, R. B. C. Sluyter, K. van Velze, and H. A. Vissenberg. 2001. Large-scale air pollution and deposition in the 'Nationale Milieuverkenning 5' (in Dutch). RIVM, Bilthoven, The Netherlands.
- Eggleton, M. A., E. L. Morgan, and W. L. Pennington. 1996. Effects of liming on an acid-sensitive southern Appalachian stream. Restoration Ecology 4:247–263.
- Ellenberg, H. 1988. Vegetation ecology of Central Europe, Cambridge University Press, Cambridge, United Kingdom.
- Fransman, B., and B. Nihlgård. 1995. Water chemistry in forested catchments after topsoil treatment with liming agents in South Sweden. Water, Air and Soil Pollution 85:895–900.

- Gimingham, C. H. 1992. The lowland heathland management handbook. English Nature, Peterborough, United Kingdom.
- Gimingham, C. H., S. B. Chapman, and N. R. Webb. 1979. European heathlands. Pages 365–386 in R. L. Specht, editor. Ecosystems of the world, 9A. Elsevier, Amsterdam, The Netherlands.
- Gunn, J., R. Sein, B. Keller, and P. Beckett. 2001. Liming of acid and metal contaminated catchments for the improvement of drainage water quality. Water, Air and Soil Pollution 130:1439–1444.
- Hagley, C. A., D. Wright, C. J. Owen, P. Eiler, and M. Danks. 1996. Changes in aquatic macrophytes after liming Thrush lake, Minnesota. Restoration Ecology 4:307–312.
- Henrikson, L., A. Hindar, and E. Thörnelöf. 1995. Freshwater liming. Water, Air and Soil Pollution 85:131–142.
- Hindar, A., R. F. Wright, P. Nilsen, T. Laessen, and R. Hogberget. 2003. Effects on stream water chemistry and forest vitality after whole-catchment application of dolomite to a forest ecosystem in southern Norway. Forest Ecology and Management 180:509–525.
- Hornung, M. 1995. The effects of natural and anthropogenic environmental changes on ecosystem processes at the catchment scale. Trends in Ecology and Evolution 10:443–449.
- Houdijk, A. L. F. M., P. J. M. Verbeek, H. F. G. van Dijk, and J. G. M. Roelofs. 1993. Distribution and decline of endangered herbaceous heathland species in relation to the chemical composition of the soil. Plant and Soil 148:137–143.
- Jansen, A. J. M., M. C. C. de Graaf, and J. G. M. Roelofs. 1996. The restoration of species-rich heathland communities in the Netherlands. Vegetatio 126:73–88.
- Kreutzer, K. 1995. Effects of forest liming on soil processes. Plant and Soil 169:447–470.
- Lorz, C., J. Hruška, and P. Krám. 2003. Modeling and monitoring of long-term acidification in an upland catchment of the Western Ore Mountains, SE Germany. Science of the Total Environment 310:153–161.
- 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.
- Menendez, R., J. L. Claytin, and P. E. Zurbuch. 1996. Chemical and fishery responses to mitigative liming of an acidic stream, Dogway Fork, West Virginia. Restoration Ecology 4:220–233.
- Mitchell, R. J., M. H. D. Auld, J. M. Hughes, and R. H. Marrs. 2000. Estimates of nutrient removal during heathland restoration on successional sites in Dorset, southern England. Biological Conservation 95:233–246.
- Nystrom, U., H. Hultberg, and B. B. Lind. 1995. Can forest-soil liming mitigate acidification of surface waters in Sweden? Water, Air and Soil Pollution 85:1855–1860.
- Porcella, D. B., C. T. Driscoll, C. L. Schofield, and R. M. Newton. 1995. Lake and watershed neutralization strategies. Water, Air and Soil Pollution 85:889–894.
- 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., E. Brouwer, and R. Bobbink. 2002. Restoration of aquatic macrophyte vegetation in acidified and eutrophicated shallow soft water wetlands in the Netherlands. Hydrobiologia 478: 171–180.
- Roelofs, J. G. M., A. J. Kempers, L. F. M. Houdijk, and Jansen, J. 1985. The effect of air-borne ammonium sulphate on *Pinus nigra* var. *maritima* in the Netherlands. Plant and Soil **84:**45–56.

- Roelofs, J. G. M., A. J. P. Smolders, T. E. Brandrud, and R. Bobbink. 1995. The effect of acidification, liming and reacidification on macrophyte development, water quality and sediment characteristics of soft-water lakes. Water, Air and Soil Pollution 85:967–972.
- Rundle, S. D., N. S. Weatherley, and S. J. Ormerod. 1995. The effects of catchment liming on the chemistry and biology of upland Welsh streams. Testing model predictions. Freshwater Biology 34:165–175.
- Schaminée, J. H. J., R. van 't Veer, and G. van Wirdum. 1995. Oxycocco-Sphagnetea. Pages 287–304 in J. H. J. Schaminée, E. J. Weeda, and V. Westhoff, editors. De vegetatie van Nederland. Deel 2. Plantengemeenschappen van wateren, moerassen en natte heiden. Opulus Press, Leiden, The Netherlands.
- Simmons, K. R. and P. G. Cieslewicz. 1996. Limestone treatment of Whetstone Brook, Massachusetts. 1. Treatment methodology and water-chemistry changes during treatment. Restoration Ecology 4:264–272.
- Soons, M. B., and G. W. Heil. 2002. Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. Journal of Ecology 90:1033–1043.

- Thompson, K., J. P. Bakker, and R. M. Bekker. 1997. Methods of seed bank analysis. Pages 23–29 in K. Thompson, J. P. Bakker, and R. M. Bekker, editors. The soil seed banks of North West Europe: methodology, density and longevity. Cambridge University Press, Cambridge, United Kingdom.
- 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 den Berg, L. J. L., Ph. Vergeer, and J. G. M. Roelofs. 2003. Restoration of heathlands in the Netherlands: the effects of turf-cut depth, aluminium and dissolved organic carbon on the germination of *Arnica montana* L. Applied Vegetation Science 6:117–124.
- van der Meijden, R. 2002. Heukel's Flora van Nederland. Wolters-Noordhoff by, Groningen, The Netherlands.
- Webb, N. R. 1998. The traditional management of European heathlands. Journal of Applied Ecology **35**:987–990.
- Westhoff, V., and E. van der Maarel. 1978. The Braun-Blanquet Approach. Pages 287–378 in R. H. Whittaker, editor. Classification of plant communities. Dr. W. Junk by Publishers, The Hague, The Netherlands.