The effectiveness of restoration measures in species-rich fen meadows

De effectiviteit van herstelmaatregelen in blauwgraslanden

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Parnassia palustris, *Juncus acutiflorus* and oil-like films of bacteria, indicating upward seepage

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Voor Ineke en mijn kinderen

Abstract

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Almost everywhere in the Netherlands species-rich fen meadows (*Junco-Molinion*) suffer from eutrophication and acidification. Consequently, biomass production has increased and many characteristic species have become locally endangered or extinct. A major cause has been the lowering of groundwater levels. This study investigates the mechanisms that control the effectiveness of hydrological restoration measures and turf stripping. The general hypothesis was that recovery of the original species-rich fen meadows requires the restoration of processes responsible for buffering the neutral soil pH and the low availability of nutrients. We conducted long-term monitoring, a fertilisation experiment and used results of hydrological modelling to analyse these processes.

We found that gradients in *Cirsio-Molinietum* plant communities are linked with drainage intensity and microtopography. Falling groundwater levels did not lead to a boosted aboveground biomass production in these fen meadows, because nutrient limitation persisted. Instead, acidification triggered a shift to more nutrient-poor plant communities, except where buffered groundwater occurred due to upward seepage. The observed acidification might be compensated by occasional inundation with base-rich surface water, which is also rich in nutrients. A single pulse fertilisation experiment showed that phosphorus (P) fertilisation brought about a change in species composition towards a community dominated by more competitive grasses. This P-induced shift in species composition declined gradually, which shows that the fen meadow can recover from incidental eutrophication.

Opportunities for the recovery of the crucial buffer mechanisms in the soil are related to upward seepage intensity. Relics of fen meadows might be too small for upward seepage to be increased sufficiently by filling in ditches in the surroundings. Hence, they suffer from infiltration of precipitation and low groundwater levels in summer. Conservation of precipitation in these small reserves is not a beneficial option, because it stimulates acidification of the topsoil. The effect of turf stripping was monitored in an acidified *Cirsio-Molinietum* during 12 years. Turf stripping exposed a nutrient-poor soil layer, with a greater acid-buffering capacity, and species from target communities had returned. However, this change was temporary since the upward seepage of base rich groundwater had weakened and internal alkalinisation was limited. Restoration measures were not effective in a formerly intensively used field. Even subterranean irrigation with deep groundwater during ten years was not sufficient to reverse eutrophication and acidification, due to irreversibly changed conditions of the clayey peat soil.

We conclude that the continuous upward seepage of base rich groundwater into the root zone is the most important prerequisite for recovering and maintaining fen meadows. The success of turf stripping in nature reserves depends on seepage intensity. Management of fen meadows needs a cyclic planning process aiming at suitable environmental conditions and with feasible target communities.

Key words: fen meadow, restoration, *Cirsio-Molinietum*, phosphorus, nitrogen, eutrophication, acidification, alkalinisation, acid-buffering capacity, groundwater.

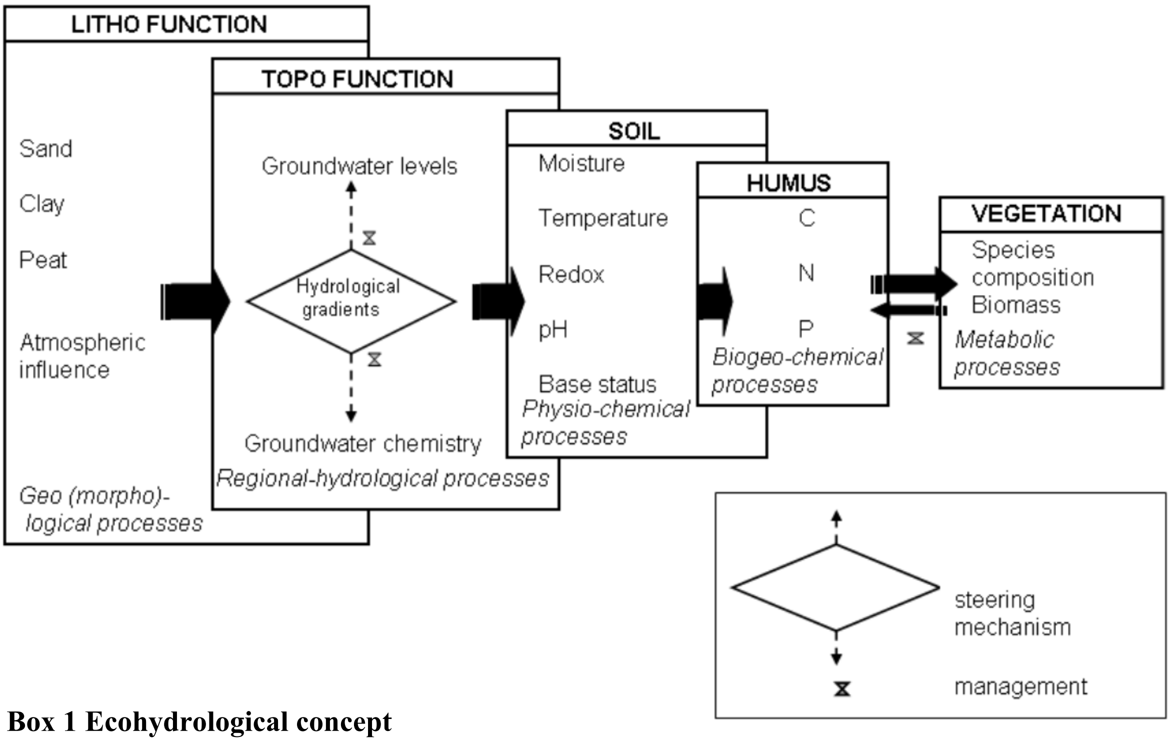
Contents

1

General introduction

Fen meadows in a changing landscape

Until 50 years ago, base-rich fens and fen meadows were common in the Netherlands. Fens are described as minerotrophic wetland vegetation on peat soils. Fen meadows are semi-natural ecosystems derived from fens by agricultural exploitation for haymaking (Wheeler 1995).



Box 1 Ecohydrological concept
Following the hierarchical structure of the ecohydrological concept, the parent material (litho function) and the topographical position (topo function) control regional hydrological processes in the landscape. Subsequently, the groundwater levels and chemical composition are determined by the spatial variation (location). Groundwater levels and chemical composition subsequently influence physio-chemical processes in the rooting zone. The resulting conditions (e.g. moisture content and pH), drive biogeochemical processes that in turn control the fluxes of the main factors controlling plant growth (e.g. nutrient availability). The concept of the hierarchy of positional, conditional and operational relationships should explain how vegetation in brook valleys and rich fens in particular is externally controlled by hydrological gradients (see Chapter 6, Grootjans et al. 1996).

Grootjans et al. (1993), Wassen (1990) and others have described the spatial variation in wet plant communities of meadows along height gradients in brook valleys and rich fens. They found a relation between the flux and quality of different groundwater flows, and between the soil fertility and the species composition and productivity of plant communities. These ecohydrological relations (see Box 1) apply if human impact has not been very strong.

Mesotrophic fen-meadow communities (so-called litter meadows) are classified as *Junco-Molinion* (Schaminée et al. 1996). Particulary the association *Cirsio dissecti-Molinietum* is species-rich and of conservational value. The *Junco-Molinion* produce 1-4 tons dry weight $ha^{-1}yr^{-1}$ and may include gradients to the more eutrophic plant communities of *Calthion palustris* and *Magnocaricion* which produce 4-8 tons $ha^{-1}y^{-1}$. This study focuses on *Junco-Molinion* (*Cirsio dissecti-Molinietum*) fen meadows including the gradient towards *Calthion.*

High groundwater levels and a supply of base-rich groundwater, achieved by the upward seepage of deep groundwater, are often a prerequisite for the buffering of wet, base-rich and nutrient-poor conditions of species-rich fen meadows in brook valleys. Moderate desiccation of the top layer during summer may occur (Jansen & Roelofs 1996). In addition, the more eutrophic fen meadows are influenced by inundation with surface water. Fertilisation experiments have shown that the aboveground biomass production of *Junco-Molinion* is often P-limited (Pegtel 1983; Egloff 1983), while most *Calthion palustris* and *Magnocaricion* meadows are N- limited (Van Duren & Pegtel 2000).

Within Dutch nature conservation policy, the importance of these hydrological factors has only fully been acknowledged since the 1980s (Grootjans et al. 1993, 1996). By then, almost everywhere in the Netherlands the relics of fen meadows had become increasingly eutrophied and acidified. Consequently, biomass production in these drained meadows had increased and many characteristic species had become locally endangered or extinct. Ecohydrological research demonstrated that an important factor in the process of eutrophication and acidification has been the lowering of groundwater, due to the exploitation of deep groundwater for drinking water and by drainage for agriculture (Runhaar et al. 1996). In addition, atmospheric nitrogen deposition and increased infiltration of precipitation water enhanced the eutrophication and acidification (Bobbink et al. 1998). Ecohydrological research had also revealed the importance of knowing both the quantitative and qualitative hydrology at various spatial scales to protect fen meadows. Therefore, ecohydrological surveys have been involved in Dutch water policy and management, since the 1980s.

Later, many restoration projects aiming to restore hydrological processes and soil conditions in disturbed fen meadows were carried out (Grootjans & Van Diggelen 1995; Wheeler 1995). With the purpose of conserving water and increasing the upward seepage of base-rich groundwater, ditches were filled in and brook water tables were raised in nature reserves and their surroundings. Moreover, to achieve less acidified and nutrient-poor conditions, turf and sods were stripped and the topsoil of former agricultural fields was even removed (Jansen & Roelofs 1996).

Jansen et al. (2000) and Grootjans et al. (2002) have evaluated Dutch projects to restore fen meadows. They concluded that sometimes restoration has been achieved with relatively little effort, while in other cases restoration has succeeded only temporarily or has failed, despite the expensive restoration measures. What the sites where measures had succeeded all had in common was a regular discharge of calcareous groundwater provided by local or regional hydrological systems, and the fact that populations of target species had been present until fairly recently. Additional restoration measures such as haymaking, rewetting and sod cutting were unsuccessful where irreversible changes in the soil profile had occurred and where soil seed banks had been completely depleted, such as in former agricultural fields. Grootjans et al. (2002) put forward some suggestions about the conditions and processes responsible for failures and success, which they derived from reviewing reports of restoration projects. However, still little is known about the biogeochemical processes that explain irreversibility and hysteresis and drive the shifts in plant communities after restoration. Such knowledge of the way that these processes operate and the required conditions is a prerequisite for the prediction of the effectiveness of measures and it cannot be derived directly from the ecohydrological concept.

Aims and approach

The aim of this study was to investigate the mechanisms that determine the effectiveness of certain measures for the restoration of species-rich fen meadows.

With the general knowledge that site conditions of species rich fen meadows are primarily characterised by a low availability of nutrients and a near neutral pH, I first investigated the biogeochemical processes in some fen meadows that bring about these characteristic nutrient-poor and acid buffered conditions. Secondly, I investigated the effects of changed hydrological conditions, initiated by disturbances or restoration measures, upon nutrient availability and acidity of soil, and the consequent shifts in plant communities.

The general hypothesis underlying this research is that the sustainable restoration of original species-rich fen meadows requires the recovery of resilience mechanisms such as acid buffering and severe nutrient limitation. Ecological resilience is the ability to return to the reference state after a temporary disturbance (Holling 1973). It is used in this study as a measure of the capacity of a fen meadow ecosystem to absorb shifts in nutrient availability and acidity caused by changes in the hydrological environment.

Within the scope of external hydrological conditions, this study examines how nutrient availability and soil acidity are controlled by groundwater level and groundwater chemistry and focuses on the effects of the upward seepage of base-rich groundwater. In addition, the response of plant communities to changes in hydrological conditions and their persistence are investigated.

Three lines of study have been followed to analyse the relevant ecosystem processes: (1) monitoring of groundwater, soil, and vegetation composition in the field; (2) experiments to determine the impacts of eutrophication; and (3) hydrological modelling to quantify the impact of hydrological measures on the intensity of upward seepage intensity, and on the level and quality of groundwater.

Fieldwork area

The study was carried out in the Bennekomse Meent nature reserve (14 ha) and the Veenkampen experimental field (13 ha), both in the south of the Gelderse Vallei, and in the Korenburgerveen nature reserve (310 ha) in the east of the Netherlands. The fen meadows in the two nature reserves consist of *Junco-Molinion* plant communities that have developed under the influence of the upward seepage of base-rich groundwater and haymaking and have been disturbed to a greater or lesser degree. They are relics of a former semi-natural landscape and are each less than 10 ha. The nature reserves are surrounded by intensively used agricultural fields and are affected by drainage, groundwater abstraction, fertilisation and increased acid deposition. Hydrological measures to restore high groundwater levels and the exfiltration of base-rich groundwater have been achieved in both nature reserves and in their surroundings.

In the Veenkampen experimental field a set-up was designed to investigate the regeneration of nutrient-poor fen meadows from intensively managed grasslands, to test the assumption that the soil conditions required could be achieved by using base-rich groundwater to raise groundwater levels.

In both areas in the south of the Gelderse Vallei the geohydrological and ecohydrological conditions were previously studied in collaboration with the Soil Physics, Agrohydrology and Groundwater Management Group from Wageningen University (Bier et al. 1992; Van der Hoek & Van der Schaaf 1988). The research in the Veenkampen experimental complex was done in collaboration with various other research groups from Wageningen University and Research Centre (WUR).

The study in the Korenburgerveen was done as part of the Survival Plan Forest and Nature (OBN) and in consultation with experts responsible for monitoring other fen meadows in the Netherlands.

Outline of the thesis

Chapter 2 examines why, in *Cirsio-Molinietum* plant communities, falling groundwater levels do not always lead to more aboveground biomass production and a shift in species composition towards more abundant tall species. The site factors responsible were selected by analysing the spatial and temporal shifts in species composition, derived from long-term monitoring. The study focuses on the relation between acidification and the succession at different spatial scales. The effectiveness of local hydrological measures is evaluated.

Chapter 3 addresses the question whether nutrient pulses may change the aboveground biomass and the plant species composition of species-rich fen ecosystems for years. It describes a single pulse fertilisation experiment with N and P in a *Cirsio-Molinietum* meadow, to investigate the persistence of these nutrient-driven shifts.

Chapter 4 presents an overview of pools and fluxes of nutrients in a fen meadow. Special attention is paid to the mechanisms buffering the nutrient-poor soil conditions in relation to groundwater level and quality. Subsequently, the impact of local hydrological measures on the recovery of high groundwater levels and upward seepage of base rich groundwater is discussed, using the predictions generated by hydrological models.

Chapter 5 focuses on the effectiveness of measures to restore the high acid buffer capacity of the soil in fen meadow sites where the upward seepage of base-rich groundwater has weakened. A field experiment on the impacts of turf stripping on external and internal alkalinisation and on the recovery of *Junco-Molinion* plant communities is described.

Chapter 6 deals with the response of the chemical composition of groundwater and soil after the rewetting of former agricultural fields. It focuses on key processes for regenerating the infertile and buffered topsoils that are prerequisites for the recovery of species-rich fen meadows. It presents the results of the monitoring in an experimental field and of some laboratory experiments.

The general discussion in Chapter 7 aims at integrating the results presented in the previous chapters and drawing general conclusions. After describing the functioning of an original, undisturbed fen-meadow ecosystem and classifying the response of fen meadows to changes in hydrological conditions, the effectiveness of restoration measures is discussed.

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2

Fen meadow succession in relation to spatial and temporal differences in hydrology and soil conditions

Van der Hoek, D. & Sykora, K.V. (*submitted to Applied Vegetation Science*)

draining ditch at the border of the fen meadow

Summary

In *Junco-Molinion* fen meadows, falling groundwater levels may not lead to a boosted aboveground biomass production if limitation of nutrients persists. Instead, depending on drainage intensity and microtopography, acidification may trigger a shift into drier and more nutrient-poor plant communities.

In a long-term study (1988-1997) along a gradient in drainage intensity, we analysed shifts in a *Junco-Molinion* in relation to the driving soil processes at different scales. We also evaluated the efficacy of various local hydrological measures for restoration.

Despite lower summer groundwater levels, aboveground biomass increased only slightly over the ten years. This was probably due to a limiting availability of nutrients: K in the well-drained plots, P in the intermediate plots, and N in the plots without drainage, plus removal of hay. *Junco-Molinion* species increased in dry sites whereas *Caricion curto-nigrae* species increased in wet sites because of soil acidification occurring when rainwater becomes more influential than base-rich groundwater. The extent of the shift in species composition depended primarily on the drainage intensity and secondarily on microtopography. Acidification resulted in the succession towards *Junco-Molinion* at the cost of *Calthion* species in drained sites. Lower in the gradient this change was counteracted by the presence of buffered groundwater. Water conservation resulted in high groundwater levels being restored in spring but not in summer. Local hydrological measures in the surroundings of the reserve largely failed to restore wetter and more basic conditions. We conclude that to conserve the typical plant communities of the *Junco-Molinion* to *Calthion* gradient in the long term, further acidification must be prevented, for example by inundation with buffered, nutrient-poor surface water.

Introduction

Cirsio dissecti-Molinietum (*Junco-Molinion*) communities, i.e. mesotrophic fen-meadow communities ("litter meadows"), were widespread in Western Europe up to the beginning of the 20th century. Nowadays, however, they are seriously threatened. This study focuses on *Junco-Molinion* fen meadows including the gradient towards *Calthion.* High groundwater levels and a supply of base-rich groundwater, achieved by the upward seepage of deep groundwater, are often a prerequisite for the buffering of the wet, base-rich and nutrient-poor conditions of species-rich *Junco-Molinion* meadows. The more eutrophic *Calthion* meadows are inundated by surface water. Fertilisation experiments have shown that aboveground biomass production and the growth of some individual species of fen meadows (*Junco-Molinion*) are often P-limited (Pegtel 1983; Egloff 1983; De Mars 1996; Güsewell & Koerselman 2002; Van der Hoek et al. 2004), while most *Calthion palustris* meadows are N- limited (Van Duren & Pegtel 2000). High-lying drained *Cirsio-Molinietum* might be limited by K (Kapfer 1988; De Mars 1996). Apart from a specific hydrological management regime, continuous removal of N and P by regular mowing is essential to conserve the required nutrient-poor conditions (Koerselman et al. 1990).

Many of the remaining *Junco-Molinion* stands are affected by intensified agricultural activities (such as drainage and fertilisation) and increased acid deposition. Drainage may result in increased mineralisation and consequently in eutrophication and boosted biomass production (Vermeer & Berendse 1983; Vermeer & Verhoeven 1987). It brings about a shift in species composition by stimulating the growth of common hayfield species and tall species (Vermeer 1986a, 1986b; Verhoeven et al. 1983; Bollens et al. 2001; Boeye et al. 1999; Ter Braak & Wiertz 1994; Van de Broek 1998). On the other hand, lower groundwater levels and the subsequent acidification may result in a succession towards *Nardo-Galion saxatalis* (Grootjans et al. 1986; ter Braak & Wiertz 1994) and biomass production decline.

Little attention has been paid to the observation that some fen meadows, biomass production has hardly changed despite drainage, while variation in species composition has occurred. Our first hypothesis is that a long-term shift towards more productive plant communities will not take place when N, P or K limitation persists despite drainage. Hydrological management and haymaking might be responsible for this persistence.

Even then, if there is acidification, species composition might vary. Our second hypothesis is that this variation in species composition can be related to abiotic conditions at two spatial scales: between sites differently affected by drainage and within sites due to microtopography.

There have been few studies of such spatial variation in vegetation changes in fen meadows at different scales: Ter Braak & Wiertz 1994; Grootjans et al. 1996; Tsuyuzaki et al. 2004. Hence, our objectives were: (1) to display the combined long-term spatial and temporal variation in the species data; (2) to interpret this variation in terms of changes in groundwater depth and soil characteristics; (3) to test whether the changes in vegetation (aboveground biomass and species composition) depend on drainage intensity and microtopography; (4) to evaluate the effectiveness of management for the maintenance of the characteristic wet, nutrient-poor conditions.

Methods

Site description

This long-term study into the dynamics of nutrient-poor *Molinietalia* plant communities as driven by water management, was done in the Bennekomse Meent (52° 01' N, 5° 36' E) nature reserve, a 14 ha remnant of former extensive communal hayfields harbouring various nutrient-poor, species-rich, fen-meadow plant communities. Nowadays the Bennekomse Meent is surrounded by heavily fertilised farmland. It is at an altitude of c. 5 m a.s.l. and lies in a former glacial valley (Figure 1), filled with fluvioglacial deposits overlain by shallow Holocene peat. The influence of calcareous groundwater upwelling from an artesian aquifer (c. 0.9 mm d^{-1}) predominates over precipitation water. A channel drains the area. The water level in this channel is regulated, so in the last decade of the 20th century inundations became less frequent. The east and south fringes of the reserve appear to be affected by the extra drainage by ditches in the adjacent pastures (Van der Hoek & Van der Schaaf 1988).

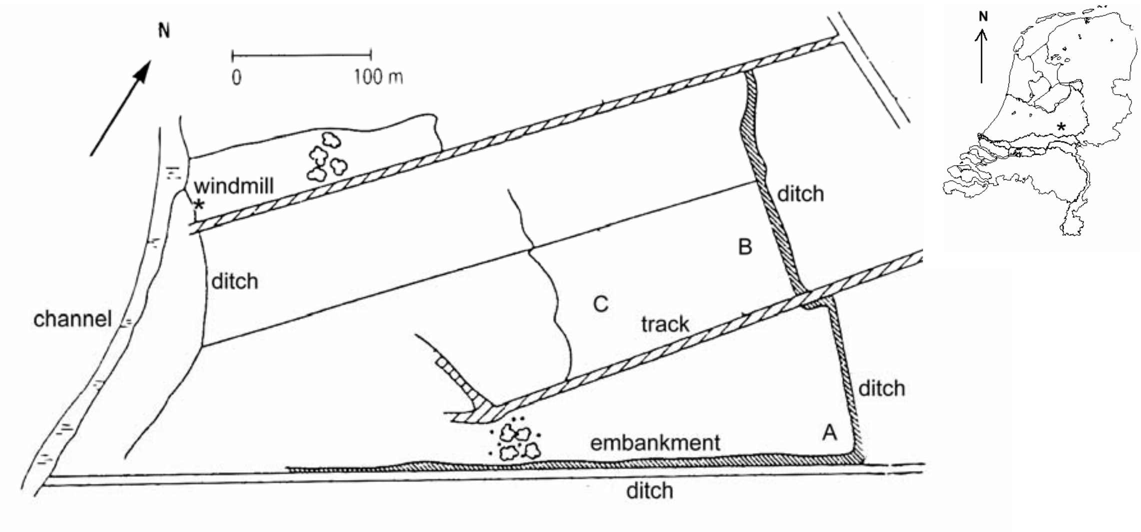

Figure 1: Location of study sites (A, B, C) in the Bennekomse Meent (*)

In order to prevent water tables falling as low as they did after several consecutive dry summers in the 1970s (Figure 2), a low embankment was constructed along the eastern and the southern borders in 1975/76, to retain water during the winter (Figure 1). A ditch was dug along one side of the embankment, to drain the adjacent farmland and to supply channel water for the restoration of high water levels in summer by groundwaterflow. In 1994/95 the boundary ditch and some ditches in the pastures around the nature reserve were made shallower, to reduce groundwater discharge and thus to stimulate the upward seepage of lithogenous groundwater (Van der Hoek & Braakhekke 1998).

Figure 2 illustrates the fluctuations of the average groundwater level in spring and the average lowest groundwater level at sites A and B in the long-term. Both levels fell in the first half of the 1970s, but rose again in response to increased summer rainfall and the change in water management. From 1985 onward the lowest groundwater level (in summer) declined steadily, but at both sites the groundwater level in spring still fluctuated around a high level. Furthermore, the average groundwater level in spring at site A systematically fluctuated below the level measured at site B after the deepening of the ditch.

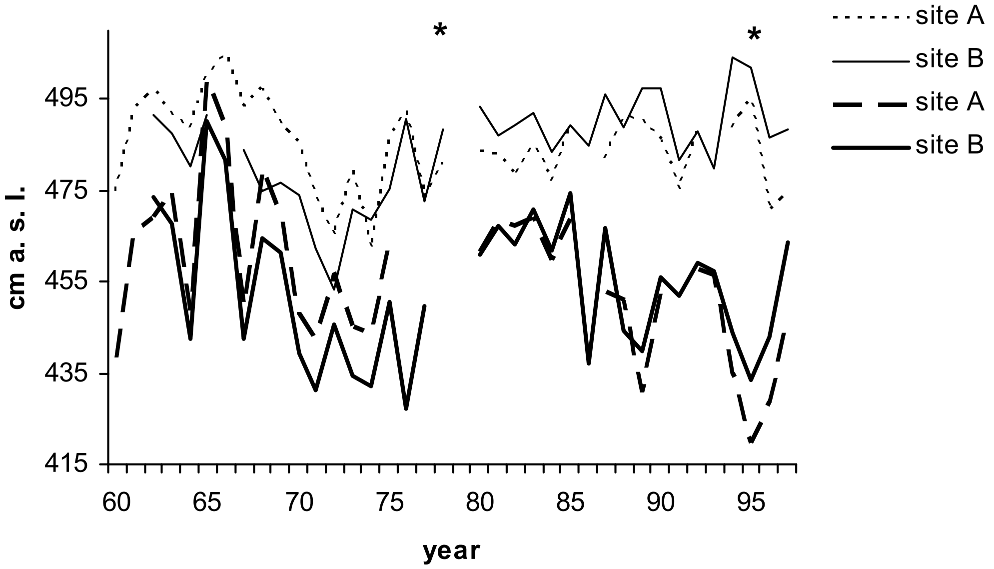

Figure 2: Average groundwater level (cm a. s. l.) in spring (thin lines) and average lowest groundwater level (thick lines), per annum (n = respectively 4 and 3) at sites A and B (dashed and solid lines, respectively). *) indicates a change in water management

We selected three sites with a *Cirsio-Molinietum* but with different hydrological conditions (Table 1, cf. Van der Hoek & Van der Schaaf 1988) on peaty soils overlying sandy subsoil. Two sites with a thin peat layer (A, B) are situated along the ditch at the eastern border of the reserve. The third, a low-lying and peaty site (C), is in the centre of the reserve. Site A, in the SE corner of the reserve is higher-lying and its groundwater levels are influenced by the drainage of the surrounding farmland and by the bordering ditch. In site B the drainage is moderate and the upward seepage of base-rich groundwater is stronger than in site A. Site C is not affected by drainage. As a consequence of standing rainwater at this site, bicarbonate concentrations in the root zone are intermediate, though upward seepage of base-rich groundwater occurs. In general, in all sites there are very shallow slopes over short distances, which are related to heterogeneity in soil conditions (thickness of peat layer) and in hydrology (depth of infiltrating rain water). In sites A, B and C we plotted 5-cm isohyps of soil surface (4 isohyps in sites A and B and 3 in site C) and within each elevation interval we laid out 4 permanent plots of 2 m x 2 m at random as replicates. In total, the vegetation and soil in 44 plots was sampled at these sites.

Table 1: Site characteristics of two drained, margin sites (A, B) and of the undrained central site (C) of the fen meadow. Values of calcium and bicarbonate concentrations in groundwater are means and SE of samples from 10, 20 and 30 cm depth.

Site characteristics	**Site A**	**Site B**	**Site C**
Elevation cm. a.s.l.	510 – 525	500 – 510	490 – 505
Thickness peat layer cm	20 – 50	20 – 50	20 – 100
Relative drainage intensity	intense	moderate	none
Average [Ca^{2+}] groundwater mg l^{-1}	56 (2)	60 (2)	56 (2)
Average [HCO_3^-] groundwater mg l^{-1}	144 (11)	198 (12)	179 (10)

Vegetation

In July 1988, 1991, 1995 and 1997 we recorded the vegetation in permanent plots in sites A, B and C according to the Braun-Blanquet cover-abundance nine-step ordinal scale (Van der Maarel 1979). Nomenclature follows Van der Meijden (1990) for phanerogams.

In July 1988, 1989, 1995 and 1997, we collected total aboveground biomass in a subarea of 0.5 m x 0.5 m in each plot of sites A, B and C, and determined the N and P concentrations in total plant material. Nitrogen and phosphorus concentrations were determined colorimetrically, after digesting the dried plant material with H_2SO_4, salicylic acid, H_2O_2 and selenium (Novozamsky et al. 1983).

Soil

In July 1988, 1991, 1995 and 1997, the soil was sampled from every plot in sites A, B and C. An undisturbed soil sample (0.1 l) was taken from the top 5 cm of each plot to determine the bulk density and for chemical analysis. Soil was sampled in addition in 1993 to determine pH-KCl. Moisture content and available P ($CaCl_2$) were measured every year during 1988–1997, except in 1994 and 1996. In addition, in the first (1988) and the last year (1997) of the study pH-H_2O, carbon content, % organic matter, total N and total P were determined as well.

A sub-sample of the soil was taken and dried at 105°C overnight to determine the moisture content. Then, samples were dried at 20°C and sieved using a 2 mm mesh. 20 g of each sample was extracted with 50 ml 1 M KCl (Houba et al. 1995) and the pH-KCl was measured in the extract using a glass electrode. Samples were extracted with a 0.01 M $CaCl_2$ solution and centrifuged (Houba et al. 1994, 1996). The supernatant was used for spectrophotometric determination of NO_3-N, NH_4-N and PO_4 by a segmented Flow Analyzer (Skalar, Breda, the Netherlands). Total amounts of N and P were determined according to the method described above for plant material. Bulk densities were used to present the results on a volume basis also (ha^{-1} to a depth of 10 cm).

Groundwater

Twice a month, groundwater levels were measured in a shallow observation well at a central point in each site. The fully perforated filter screens of the four observation wells are between the surface and 2 m depth. Data on the groundwater levels of sites A and B have been collected since 1960. For each site, the average groundwater level in spring (March and April) and the average of the three lowest groundwater levels per annum were calculated, both with respect to sea level and soil surface. The average of both variables over two consecutive years at all permanent plots was calculated using the levelled elevation of the plots.

In each site in a high and low plot we installed two ceramic soil moisture samplers with a porous length of 10 cm and a vacuum syringe to measure the chemical composition of groundwater at depths of 10, 20 and 30 cm. During 1989–1996 the groundwater was sampled twice a year, in winter and in summer. The samples were stored at 4 °C in the dark and analysed the next day. Ca^{2+} was determined by flame atomic absorption spectrometry (AAS). HCO_3^- was analysed colorimetrically, using a continuous flow analyser (SKALAR SAN plus system).

Data analysis

Multivariate analysis was used to analyse the shifts in species composition, the spatial distribution of the vegetation and to investigate the relation between species composition and environmental variables.

To allow description of the vegetation change in terms of plant communities, the relevés of the different years had to be classified first. After classification the syntaxonomic change of each relevé over time could be described. The vegetation data (176 relevés, 88 species) were clustered using TWINSPAN (Hill 1979). First, four levels of division were applied to obtain a limited number of clusters. Subsequently, a preliminary synoptic table was made. Species were grouped into syntaxonomic elements (groups of species, characteristic for particular syntaxa) and the average cover/abundance value of each syntaxonomic element was calculated. For this purpose, the sum of the cover/abundance values of the species from one syntaxonomic element per relevé was divided by the number of all characteristic species of that specific element present in the vegetation table. Clusters with similar syntaxonomic composition were combined using a DCA ordination diagram. The six resulting plant communities were summarised into a final synoptic table (Appendix), showing presence classes and the cover of the species in the different clusters and were named according to Schamininée et al. (1995, 1996).

Detrended Correspondence Analysis (DCA), Hill 1979) of all separate relevés was used to show the main variation in species composition of the three sites. Afterwards the indicated site conditions according to Ellenberg et al. (1992) and the proportion of syntaxonomical elements were used as explanatory variables (predictors) for indirect gradient analysis and interpretation of the ordination axes (Ter Braak and Smilauer 1998).

To investigate the relation between change in species composition during the ten-year period and the environment, we also performed a direct ordination (canonical correspondence analysis: CCA) with the datasets of 1988 and 1997. A covariable for each plot was used to filter out the spatial variation factor. For this analysis we used only the variables with a significant difference between both years (t-test). Forward selection of variables was used to build a model to explain the total variance and to investigate the hierarchy of the selected master factors. Monte Carlo permutation tests were carried out for all variables to test for significance 199 permutations and a significance level of 0.05). All environmental variables were tested for Gaussian distribution (Kolmogorov-Smirnov test). In order to achieve homogeneous variances, some data were ln-transformed.

Finally, we performed an indirect ordination on data of the start (1988) and the end of the time series (1997) only, to analyse and show the overall shift in vegetation in relation to the master factors.

The effects of drainage (site), elevation and year on the abiotic data and on the proportion of syntaxonomic elements were analysed using repeated measures analysis of variance (ANOVAR; Potvin et al. 1990), with site as the between-subject factor, year as the within-subject factor and relative elevation as covariate. SPSS for Windows (8.0) was used for these calculations, and for the calculation of the correlation (Pearson) between variables.

Results

Plant communities

The following six plant communities were distinguished (for diagnostic species, see the synoptic table in Appendix 1):

1,2. *Cirsio dissecti-Molinietum nardetosum (Junco-Molinion)*

Plant communities 1 and 2 are differentiated by respectively *Cardamine pratensis*, *Rumex acetosa, Cirsium palustris*, *Succisa pratensis, Lotus uliginosus, Valeriana officinales, Lysimachia vulgaris* (community 1) and with low frequency by *Achillea ptarmica*, *Ranunculus flammula*, *Lathyrus palustris* (community 2). *Carex hostiana* is more abundant in community 2 than in community 1.

3. *Crepido-Juncetum (Calthion)*

4. *Cirsio dissecti-Molinietum nardetosum / Caricion curtae agrostietum caninae* characterised by the species of community 1 but in combination with many *Parvocaricetea* species

5. *Cirsio dissecti-Molinietum / Crepido Juncetum*. This community is a transition between the *Junco-Molinion* and the *Calthion*. Both diagnostic species of the *Junco-Molinion* and of the *Calthion* occur.

6. FC *Cirsio dissecti-Molinietum / Caricion curtae agrostietum caninae*. This frame community (Basal community sensu Kopecky & Hejny 1978) forms a transition between the *Junco-Molinion* (community 2) and the *Caricion nigrae* and is characterised by the presence of differential and characteristic species of the *Junco-Moli*nion plus *Calthion* species. It is further characterised by the absence of *Valeriana dioica*, *Succisa pratensis* and *Festuca* ovina and by the relatively high presence class of *Eriophorum angustifolium.*

Changes in the vegetation

Spatial variation in vegetation

The DCA biplot (Figure 3) shows both the spatial gradient and the temporal development of the vegetation, since it has been derived from all data collected between 1988 and 1997. The relations between the main variation in species composition and the proportions of syntaxonomic elements and the average Ellenberg indicator values for the status of the soil (Ellenberg et al. 1992) are presented in the biplot as arrows. The combined proportion of the *Filipendulion* and *Phragmition* species is labelled as the variable “tall herbs”. The biplot accounts for 26 % of the total variance of species data. The third axis explained only an additional 4 % of the variance.

The main gradient (axis 1) is related to a gradient from *Junco-Molinion* to *Calthion*. The second axis is related to variation in the *Parvocaricetea* element. In terms of indicated site conditions, the main gradient can be considered to be a “buffer and productivity gradient” from poorly buffered acidic and poorly productive *Junco-Molinion* sites to well-buffered neutral and more productive *Calthion* sites. The coefficients of determination along the first axis are 81 % for the *Calthion* values, 37 % for the *Junco-Molinion* values, 77 % for the nutrient values and 54 % for the reaction values.

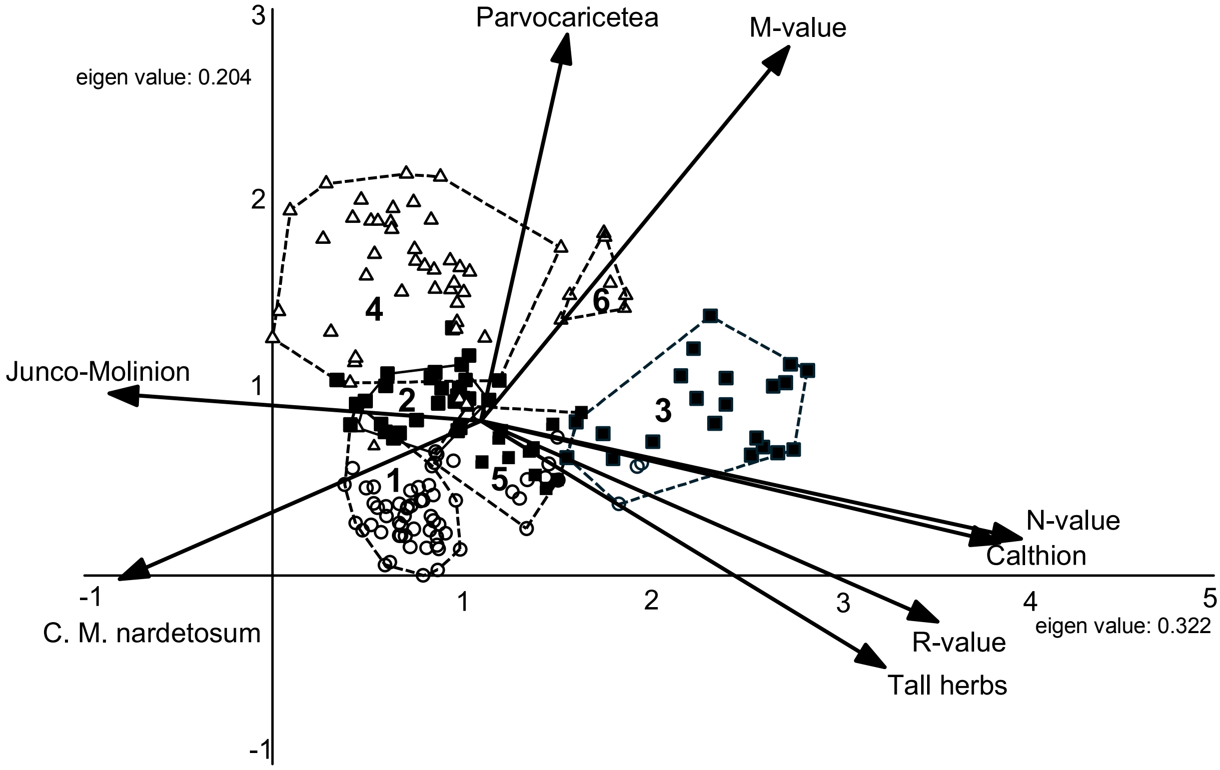

Figure 3: DCA ordination diagram (first two axes) of all relevés 1988–1997. Plant communities distinguished are outlined. The relation between syntaxonomical elements, tall herbs, Ellenberg figures (**M**oisture, **N**utrient and **R**eaction values) and the first two axes is indicated by arrows.
Plant communities: 1, 2 = *Cirsio dissecti-Molinietum nardetosum (Junco-Molinion)*, 3 = *Crepido-Juncetum (Calthion)*, 4 = *Cirsio dissecti-Molinietum nardetosum/ Caricion curtae agrostietum caninae*, 5 = *Cirsio dissecti-Molinietum /Crepido Juncetum*, 6 = FC *Cirsio dissecti-Molinietum / Caricion curtae agrostietum caninae*. Relevés are represented by symbols relating to sites: O = site A, ■ = site B, Δ = site C.

Reaction values, nutrient values, abundances of *Calthion* and tall herbs species are positively correlated, as are the moisture value and *Parvocaricetae* (p= 0.01; two-tailed). The abundance of *Junco-Molinion* is negatively correlated with reaction values, the abundances of *Calthion* and tall herb species.

ANOVAR (Table 2) showed that the effects of drainage (i.e. site) are highly significant on all the variables presented. The biplot, Figure 3, shows that characteristic species of the *Junco-Molinion* (*Cirsio dissecti-Molinietum nardetosum*, plant community 1) are most abundant in the driest site, with intense drainage (site A). Plant community 4, characterised by a strong *Parvocaricetea* element, is dominant in the wettest site, with no drainage (site C). The vegetation in these sites is relatively homogeneous and indicates less buffered conditions and less availability of nutrients (R- and N-values cf. Ellenberg et al. 1992). The moderately drained site B, by contrast, harbours all the plant communities distinguished. Its scatter along the first axes indicates the presence of both less buffered and more buffered conditions.

Table 2: Significant effects of drainage and elevation by year on the proportion of syntaxonomic elements and on the calculated Ellenberg indicator values of the plant communities in sites A, B and C during 1988–1997. ANOVAR, using drainage and year as between and within factor, respectively, and elevation as covariate. Level of significance: * p < 0.05, ** p < 0.01, *** p < 0.001.

	between effects		within effects		
	elevation	**drainage**	**yr**	**yr x elevation**	**yr x drainage**
N-value	***	**		*	*
R-value	***	***	*		**
M-value	***	***			
Junco-Molinion	***	**	*		**
Calthion palustris	***	***			
Parvocaricetea	**	***	**		
C.M.-nardetosum	***	***	*		*
Tall herbs	***	***			**

As far as the spatial variation within sites is concerned, the effects of elevation are significant on all the variables presented (Table 2). Plant community 2 occurs on the highest plots of the moderately drained site B while the *Calthion* (plant community 3) dominates in its low plots. On the lowest plots of the undrained site C the frame community (6) occurs and forms a transition from plant community 4 towards the *Cathion* community. At mean elevation in the moderately drained site B the transition type, plant community 5, occurs. Tall herbs are most abundant in the lowest plots of intensely and moderately drained sites (A and B, respectively), which may be more eutrophic since higher N-values were found here. In general, the *Junco-Molinion* element increases with increasing elevation; concomitantly, the *Calthion* and *Parvocaricetea* elements and the abundance of tall herbs decrease. These gradients are most clear in the moderately drained site B and indicate heterogeneity in soil conditions, in accordance with the M-, R- and N values we found.

Succession

Apart from spatial variation, Figure 4 (based on Figure 3) illustrates the dependence of vegetation change during 1988–1997 on drainage intensity (site). Using ANOVAR (Table 2), it was possible to test the significance of temporal effects and to search for significant year x drainage interactions. Figure 4 and the interaction year x drainage (Table 2) illustrate that an increase of the *Junco-Molinion* and *C.M.-nardetosum* was found in particular on the moderately drained site B. In addition, an overall increase of the *Parvocaricetea* element over the years was found. This is especially clear in site C (Figure 4). The *Parvocaricetea* element is mainly represented by *Caricion nigrae* species, such as *Eriophorum angustifolium* and *Hydrocotyle vulgaris*, indicating more acid conditions. No changes in the abundance of *Calthion* species occurred (no significant year-effect was found), although a decline is suggested by the biplots in the moderately and undrained sites. For tall herbs, the significant interaction year x drainage is mainly caused by the decline in the site with no drainage (site C). No striking changes were found in the cover of other high-yielding species since 1988. *H. lanatus* was most abundant in site B and its cover increased slowly over time there, but never exceeded 5 % in any site after 1988.

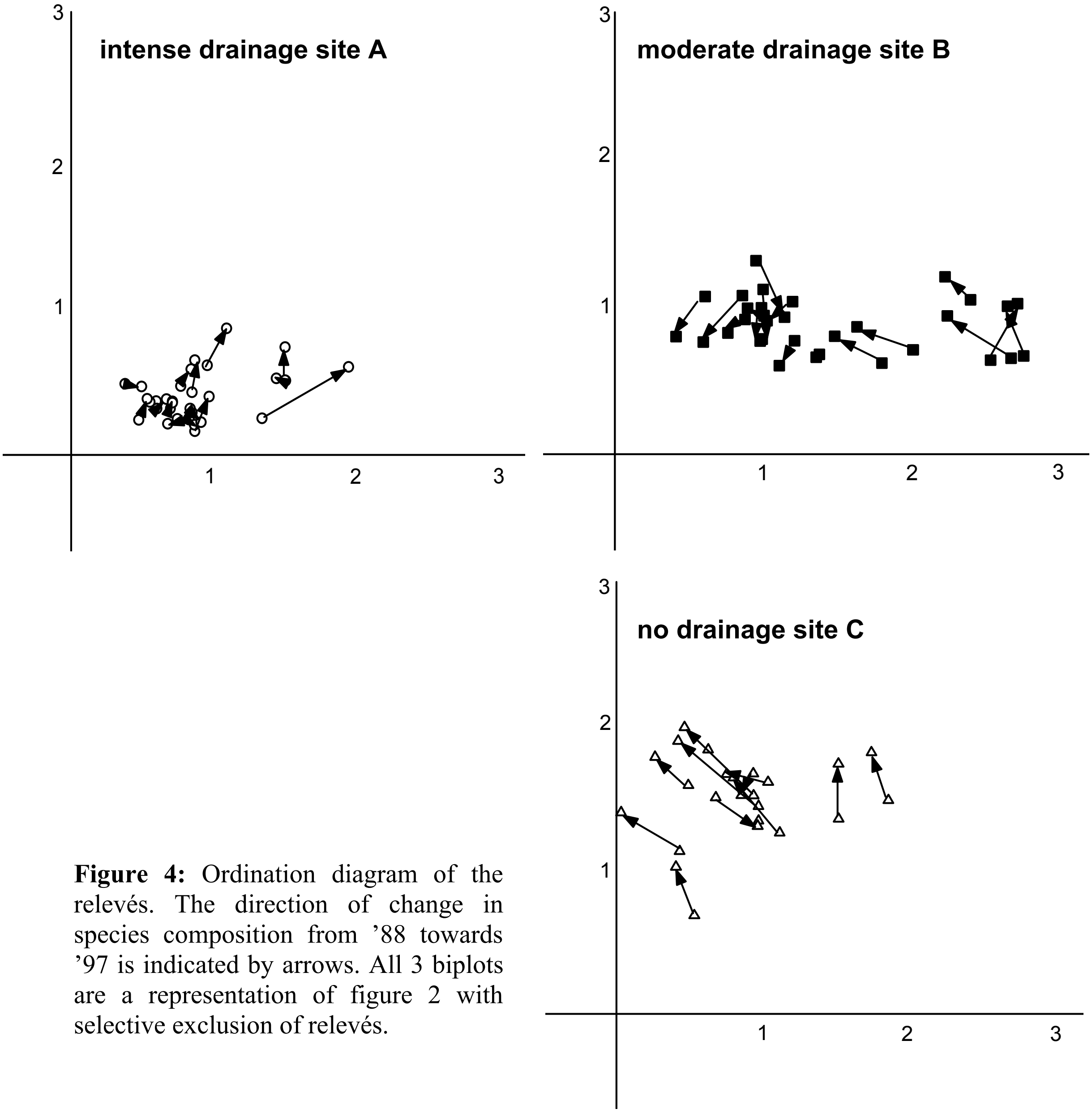

Figure 4: Ordination diagram of the relevés. The direction of change in species composition from '88 towards '97 is indicated by arrows. All 3 biplots are a representation of figure 2 with selective exclusion of relevés.

With the exception of the intensely drained site (A), the succession indicates an overall decrease of the buffering capacity (Reaction value) in time (Figure 4), which is in agreement with the significant year effect and the interaction between year and drainage (Table 2). In the lowest plots of the moderately drained site and also in the site with no drainage, there was in addition a decrease of N-values.

Relation with environmental factors

A significant effect of drainage and elevation on bicarbonate concentrations of groundwater was found ($p < 0.01$ and $p < 0.001$, ANOVA), showing that less buffered and more buffered conditions co-exist between and within the sites. The lowest concentrations occur in high plots of the intensely drained site A (post hoc Tukey test). The calcium concentration of groundwater was significantly affected by elevation ($p < 0.001$, ANOVA), with the values being higher in low plots.

Between 1988 and 1997, there was a significant decrease in the pH (H_2O, KCl), total-N and total-P (both by kg^{-1} and ha^{-1}), available-P (kg^{-1}) in soil, N- and P concentration in plant material, average groundwater level in spring and average lowest groundwater level (t-test, not shown). The increase in aboveground biomass was significant but small (from 313 ± 9 to 372 ± 11 g m^{-2}).

CCA with forward selection (using plot as a covariable) on the data from 1988 and 1997 (sites A, B and C), revealed that species composition was significantly related to pH-KCl, soil-available P, average lowest groundwater level, tissue P concentration, soil mineral N and aboveground biomass. Together, these master factors appeared to explain 8 % of the variation remaining after accounting for the spatial variation (covariable plot). The spatial variation explained 69 % of the variance in species data.

In the biplot of an indirect gradient analysis (DCA: Figure 5) using the selected master factors and after accounting for plot (covariable), the relevés of both years are clearly separated along the first axis. The plot clearly shows that after eliminating variation attributable to differences between plots, species composition changed from 1988 to 1997. Together, both axes of the biplot explain 22 % of the variance. The coefficients of determination for the variables pH-KCL, P concentration in plant material, mineral-N in soil, average lowest groundwater level, aboveground biomass and available-P along the first axis are 67 %, 65 %, 60 %, 46 %, 42 % and 18 %, respectively. The biplot illustrates not only that aboveground biomass and mineral-N in soil increased over time and average lowest groundwater level fell (i.e., a deeper groundwater level in summer), but also that pH-KCl, available P in soil and P-concentration in plants decreased.

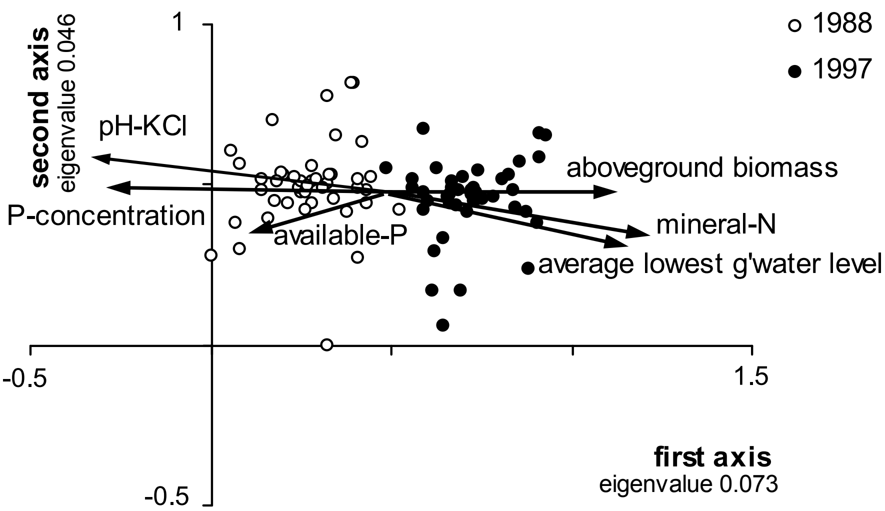

Figure 5: Position of relevés of sites A, B and C (1988 and 1997) in relation to the influence of the master factors, for the first two axes of a Detrended Correspondence Analysis. A covariate for each plot was used to filter the spatial variation.

The spatial and temporal variations during 1988–1997 in the above-mentioned selected factors are significantly determined both by drainage (i.e. site) and year (ANOVAR: Table 3). In addition, pH-KCl and available P in the soil show a significant decrease with increasing elevation, emphasising the drainage effect (Table 3, Figure 7).

Table 3: Significant effects of drainage and elevation by year on selected master factors in sites A, B and C during 1988–1997. Level of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (ANOVAR).

	between effects		**within effects**		
	elevation	**drainage**	**yr**	**yr x elevation**	**yr x drainage**
pH-KCL	**	***	**		
Available-P mg kg^{-1}	***	***	***	*	*
Depth of average lowest groundwater level		***	*		
P concentration in plant g kg^{-1}		***	**		
Mineral-N mg kg^{-1}		***			
Biomass g m^{-2}		*	**		**

The values of pH-KCl and available-P are lowest in the intensely drained site A and highest in site C, which is not drained (Figures 6 and 7, respectively). The pH-KCl decreased over time in all sites, especially in site A. Available P fluctuated strongly from year to year. The significant interaction year x drainage and year x elevation points to the low and decreasing values of available P at site A, especially in the high plots (figure 7): the lowest values are for the highest plots of site A. The values of available P in the lowest plots of site A resemble the plots of moderately drained site B, except for the highest plots, which have values similar to those found in the high A plots (Figure 7, at $\alpha = 0.05$, Tukey's post-hoc test).

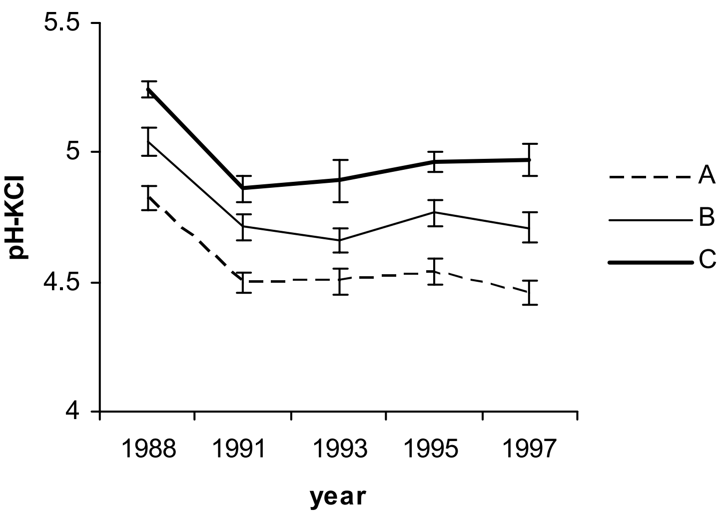

Figure 6: pH-KCl in the soil (0-5 cm depth) of permanent plots at sites A, B and C during 1988–1997. Values are means ± SE (n = 16, 16 and 12 respectively).

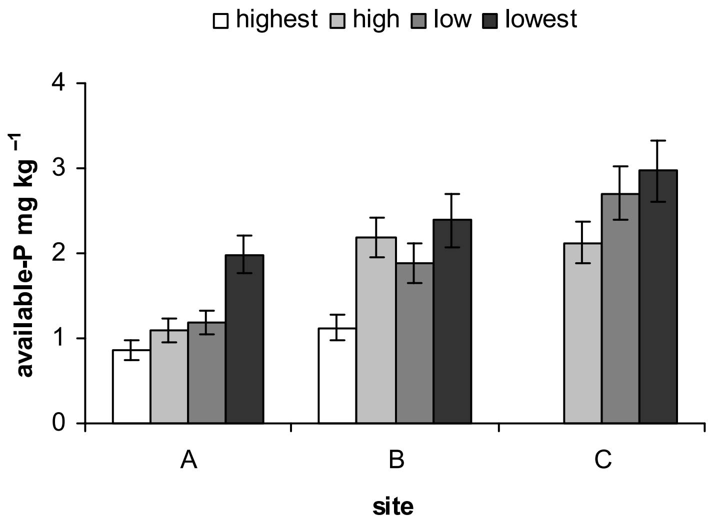

Figure 7: Available P (mg kg^{-1}) in the soil (0-5 cm depth) of permanent plots at different elevation (highest-lowest cf. 5 cm isohyps) at sites A, B and C. Values are means during 1988 –1997 ± SE (n = 32).

The significant drainage effect points to the small aboveground biomass in undrained site C (Table 3). Figure 8 and the significant year effect together with the significant interaction year x drainage point to the increase of aboveground biomass over time in sites A and B.

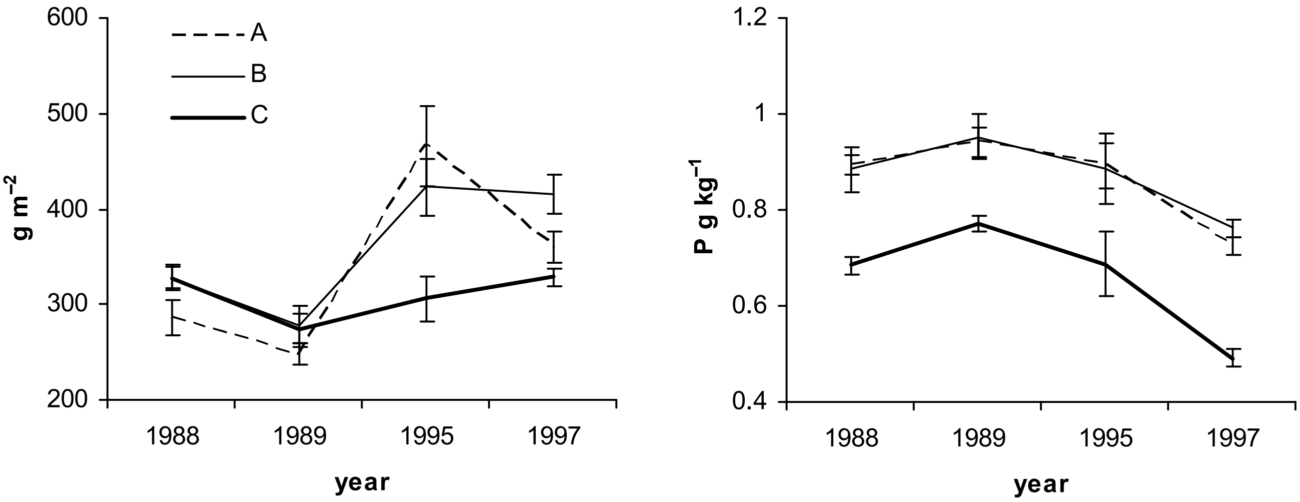

Figure 8: Aboveground biomass (g m^{-2}) and P concentration (g kg^{-1}) in plant material of permanent plots at sites A, B, and C. Values are means during 1988–1997 ± SE (n = 16, 16 and 12 respectively).

An overall effect of year on P concentration in plant material was found (ANOVAR: Table 3) which corresponds with the gradual decrease of the P concentration in plant material at all sites (Figure 8). In addition, a significant drainage effect was found, with low P concentration in plants at site C.

Discussion

Our long-term study in *Molinietalia* plant communities shows that despite drainage, there was only a limited increase of aboveground biomass (on average from 313 ± 9 to 372 ± 11 g m^{-2}), together with an increase of *Junco-Molinion* and/or *Caricion nigrae* species that indicated more acid, but still nutrient-poor, conditions.

The persistence of nutrient-poor conditions

Our finding that lower groundwater levels did not lead to a rapid increase in biomass production since limiting nutrients did not become more available supports our first hypothesis. We attribute such a limited increase of biomass to P primarily limiting plant production in our fen meadow. The P limitation is suggested by the P concentration in plant material and the soil-available P decreasing gradually (Figure 5), whereas aboveground biomass hardly increased; this has also been observed in other wet meadows (De Mars 1996, Van Duren et al. 1997, Van Duren & Pegtel 2000). P limitation seems plausible, as when the soil of wet meadows becomes drier and aerated, phosphate immobilisation in iron phosphate complexes increases (Grootjans et al. 1986: cf. Patrick and Khalid 1974, Van der Hoek & Braakhekke 1998). An additional explanation for the persistence of P limitation might be the export of P by hay removal (Koerselman et al. 1990, Olff and Pegtel 1994, Van der Hoek et al. 2004).

In drained plots, however, the aboveground biomass might be limited by potassium, since we found that in moderately drained plots more available P does not lead to increased production of aboveground biomass (Figures 7 and 8). This finding agrees with the results of the N and P fertilisation experiment on the moderately drained site, which showed neither P- nor N limitation (Van der Hoek et al. 2004). Kapfer 1988 and De Mars 1996 also concluded that after haymaking for many years, potassium might have become in short supply in *Cirsio-Molinietum*, as a consequence of a drainage-induced leaching.

In the low plots without drainage, small sedges dominate and the aboveground biomass is limited by N (Van der Hoek et al. 2004) and did not increase over time. Normally, little N is available in soil here, as little N can be released because high groundwater levels prevail (Van der Hoek & Braakhekke 1998). The absence of a significant year effect (Table 3) shows that nitrogen-poor conditions persisted here too, probably because of the recovery of the high groundwater levels in spring (Figure 1). We attribute the presence of much available P in the soil in low plots (Figure 7) to a low uptake as well as to the prevailing reductive conditions (Patrick and Khalid 1974).

We conclude that nutrient-poor conditions persisted over time, despite drainage. Depending on drainage conditions and microtopography, different sites in which biomass production is limited by N, P or K may co-exist over long periods. However, the differences in aboveground biomass production due to drainage are small and are not influenced by microtopography. Even the effects of temporarily increased nutrient supply, i.e. an increased growth of common hayfield species such as *Holcus lanatus*, faded away in time (van der Hoek & van der Schaaf 1988; unpublished data G. Londo), due to the buffering of soil and removal of nutrients by haymaking (Van der Hoek et al., 2004). Haymaking is likely to be an important factor to maintain the nutrient-poor conditions that limit aboveground biomass production in all plots of our fen meadow.

Acidification-driven shifts in plant communities

Acidification and nutrient depletion by haymaking resulted in a succession towards *Junco-Molinion* at the cost of *Calthion* elements and an increase of the *Parvocaricetea* element in the low plots. The acidification should primarily be attributed to the lower groundwater in summer (Figures 1, 5) and the increased influence of rainwater in the root zone.

In correspondence with our second hypothesis, shifts in plant communities occurred that depended on drainage intensity and elevation. We found such spatial variation in vegetation changes at different scales. Intense drainage stimulated acidification and resulted in a relatively homogeneous nutrient-poor *Junco-Molinion* with a *Cirsio-Molinietum nardetosum* on high plots. Due to intense drainage and acidification, the succession towards this plant community has accelerated since the 1970s (cf. unpublished data G. Londo) and resulted in the disappearance of characteristic more eutrophic *Calthion* species (cf. Grootjans et al. 1996). In the moderately drained site, representatives of all the plant communities distinguished persisted. Here, since the soil is more buffered than in the intensely drained site due to higher concentrations of bicarbonate in the groundwater, elements of the *Junco-Molinion* and the *Calthion* are able to co-exist, depending on the microtopography variation in elevation (Table 2). In the absence of drainage, rainwater ponds on the plots (whether low- or high-lying); the species composition responds to this by converging via an increase in *Parvocaricetea* mainly represented by acidophilic *Caricion nigrae* species. Van Diggelen et al. (1991) and Bakker et al. (1987) also observed that the root zone of a small-sedge meadow may acidify within a few decades (Bakker et al. 1987).

In conclusion, we attribute the sustainability of our *Cirsio-Molinietum* despite the persistence of low groundwater levels in summer caused by drainage, to gradients towards the *Calthion* that are slowly moving downward. The succession is driven by an increasing influence of acid rainwater at the cost of base-rich groundwater in the root zone, which is conditioned by drainage intensity and elevation.

Implications for water management

Partly due to the absence of dry years, local hydrological measures have raised the groundwater levels in spring. As a result, nitrogen-poor conditions have persisted in low plots, due to limited nitrification. However, despite water conservation and the filling in of ditches in the surroundings of the nature reserve, in the 10 years of our study the annual lowest groundwater levels continued to fall and the upward seepage of calcareous groundwater did not increase. Water conservation reduced the upward seepage, allowing more infiltration of acid precipitation water (Van der Hoek & Van der Schaaf 1988). The restoration of wetter and more basic conditions has only succeeded locally, in low plots near the boundary ditch, and has been achieved because the drainage has weakened. However, the success might be short-lived. Effective upward seepage can only be realised in this nature reserve if the reserve is enlarged (Van der Schaaf 1998). Finally, we conclude that due to haymaking and the drainage-induced acidification, fen meadows may evolve into more acidic, nutrient-poor, *Junco-Molinion* plant communities, still rich in species, without aboveground biomass production increasing. As a consequence of differences in drainage intensity and elevation, different states may co-exist in the long-term. We expect an increase of the *Cirsio-Molinietum nardetosum* and possibly the development of *Nardo-Galion saxatilis* in high plots. The high cover of the moss *Rhytidiadelphus squarrosus*, found by Londo (2002) in this *Junco-Molinion* stand, can prevent seedlings from establishing (Van Tooren et al. 1987), however, and hence retard this succession (Bakker et al. 2001). Nevertheless, the *Junco-Molinion* will continue to exist in the reserve in the future, although migration to lower plots might occur. A promising option for its conservation is to prevent further acidification, by inundating with buffered surface water (De Mars 1996). If only eutrophic surface water is available, the inundation has to be restricted to low plots, to maintain the *Calthion* elements. To maintain the *Cirsio-Molinietum* communities, inundation with N- and P-rich water must be only incidental (Van der Hoek et al. 2004).

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APPENDIX

Synoptic table of the communities distinguished.

Percentage presence is given as well as mean cover (superscript).

The percentage presence is expressed in six classes: + = 0-5%; I = 6-20%; II = 21- 40%; III = 41-60%; IV = 61-80%; V= 81-100%.

For calculation of mean cover the ordinal values are used.

Species differentiating between the different clusters are indicated with a gray background.

Negatively differentiating species are boxed (criterion for differentiating: 30%).

Plant communities:

1, 2 *Cirsio dissecti-Molinietum nardetosum (Junco-Molinion)*

3. *Crepido-Juncetum (Calthion)*

4. *Cirsio dissecti-Molinietum nardetosum / Caricion curtae agrostietum caninae*

5. *Cirsio dissecti-Molinietum / Crepido-Juncetum*

6. *FC Cirsio dissecti-Molinietum / Caricion curtae agrostietum caninae*

Plant community	**4**	**1**	**2**	**5**	**6**	**3**
Number of releves	45	50	25	25	7	24
Mean number of species	20.2	25.6	25.8	28.6	22.4	28.0
Standard deviation	4.7	3.4	4.0	3.3	2.4	3.8
MOLINIO-ARRHENATHERETEA						
Anthoxanthum odoratum	IV ^{2}	V ^{3}	V ^{3}	V ^{3}	II ^{2}	V ^{3}
Holcus lanatus	III ^{2}	IV ^{2}	V ^{3}	V ^{3}	I ^{2}	V ^{3}
Festuca rubra	I ^{3}	V ^{4}	IV ^{4}	V ^{3}	I ^{4}	II ^{4}
Plantago lanceolata	I ^{2}	V ^{4}	V ^{2}	V ^{3}	-	II ^{2}
Ranunculus acris	I ^{2}	IV ^{2}	V ^{2}	V ^{2}	I ^{1}	V ^{2}
Prunella vulgaris	II ^{2}	IV ^{2}	V ^{2}	III ^{2}	I ^{2}	III ^{2}
Cardamine pratensis	II ^{2}	IV ^{2}	II ^{2}	IV ^{2}	III ^{2}	IV ^{2}
Centaurea jacea	II ^{1}	V ^{3}	IV ^{2}	V ^{3}	I ^{2}	II ^{2}
Rumex acetosa	+ ^{1}	III ^{2}	-	IV ^{2}	-	IV ^{2}
Ranunculus repens	+ ^{2}	+ ^{1}	-	-	-	III ^{3}
Poa trivialis	-	-	-	-	-	II ^{3}
Lathyrus pratensis	-	+ ^{2}	+ ^{2}	-	-	-
MOLINIO-ARRHENATHERETALIA						
Phleum pratense	-	-	-	-	-	I ^{2}
MOLINIETALIA						
Cirsium palustre	-	IV ^{2}	+ ^{1}	II ^{2}	I ^{1}	+ ^{1}
Equisetum palustre	V ^{2}	IV ^{2}	V ^{2}	IV ^{2}	IV ^{1}	V ^{2}
Juncus conglomeratus	III ^{3}	I ^{3}	II ^{2}	III ^{2}	II ^{4}	IV ^{3}
Luzula multiflora	I ^{1}	V ^{3}	IV ^{2}	V ^{2}	I ^{1}	II ^{2}
Galium uliginosum	III ^{2}	IV ^{3}	V ^{3}	V ^{3}	III ^{3}	IV ^{3}
Valeriana dioica	II ^{2}	V ^{3}	V ^{3}	IV ^{3}	-	II ^{3}
Achillea ptarmica	I ^{1}	+ ^{2}	II ^{2}	II ^{2}	III ^{2}	IV ^{2}

APPENDIX continued

Plant community	4	1	2	5	6	3
JUNCO-MOLINION						
Succisa pratensis	III 2	V 5	II 2	III 2	-	I 1
Juncus conglomeratus	III 3	I 3	II 2	III 2	II 4	IV 3
differentiating species with respect to **CALTHION**						
Molinia caerulea	V 6	V 6	V 7	V 6	V 6	III 5
Potentilla erecta	V 3	V 4	V 2	IV 3	IV 2	II 3
Agrostis canina	V 3	V 2	V 4	V 4	V 4	V 4
Gentiana pneumonanthe	II 1	I 1	II 2	I 2	I 1	-
Luzula multiflora	I 1	V 3	IV 2	V 2	I 1	II 2
Viola palustris	+6	-	-	-	-	-
Valeriana dioica	II 2	V 3	V 3	IV 3	-	II 3
Cirsio Dissecti-Molinietum						
Cirsium dissectum	V 5	IV 3	V 4	IV 3	V 3	II 3
Carex panicea	V 6	V 5	V 5	V 5	V 6	II 5
Carex hostiana	IV 3	I 2	III 3	I 2	-	I 2
Carex pulicaris	I 3	+1	-	-	-	-
Cirsio Dissecti-Molinietum nardetosum						
differentiating species						
Danthonia decumbens	IV 2	IV 2	IV 2	I 3	I 1	I 2
Festuca ovina	I 3	V 4	III 4	II 3	-	II 3
Viola canina	II 2	II 2	I 3	II 3	I 2	I 2
Cirsio Dissecti-Molinietum peucedanotosum						
differentiating species						
Hydrocotyle vulgaris	II 3	+1	+2	+5	I 6	+5
Calamagrostis canescens	I 3	+2	I 2	II 2	III 2	IV 4
Phragmites australis	III 2	III 2	IV 2	IV 2	I 1	III 2
Juncus subnodulosus	I 1	+1	-	-	I 2	-
Cirsio Dissecti-Molinietum parnassietosum						
differentiating species						
Dactylorhiza majalis	+2	-	I 1	I 1	-	I 1
CALTHION						
Lychnis flos-cuculi	-	-	-	I 2	I 1	II 2
Dactylorhiza majalis	+2	-	I 1	I 1	-	I 1
Lotus uliginosus	I 1	IV 2	II 2	V 2	III 2	IV 3
Caltha palustris subsp. p	I 2	-	I 2	I 2	III 2	IV 4
Rhinanthus angustifolius	I 1	II 1	II 1	IV 1	-	IV 2
Carex disticha	II 3	I 2	I 3	III 3	III 2	IV 3
differentiating species with respect to **JUNCO-MOLINION**						
Myosotis palustris	+2	-	I 1	I 2	-	II 2
Ranunculus repens	+2	+1	-	-	-	III 3
Poa trivialis	-	-	-	-	-	II 3

APPENDIX continued

Plant community	**4**	**1**	**2**	**5**	**6**	**3**
Crepido-Juncetum Acutiflori						
Juncus acutiflorus	I ^{2}	-	I ^{2}	+^{2}	-	-
optimum in ***Crepido-Juncetum Acutiflori***						
Galium uliginosum	III ^{2}	IV ^{3}	V ^{3}	V ^{3}	III ^{3}	IV ^{3}
Juncus conglomeratus	III ^{3}	I ^{3}	II ^{2}	III ^{2}	II ^{4}	IV ^{3}
Achillea ptarmica	I ^{1}	+ ^{2}	II ^{2}	II ^{2}	III ^{2}	IV ^{2}
Ranunculo-Senecionetum aquatici						
Senecio aquaticus	-	-	-	+^{1}	-	I ^{1}
differentiating species						
Ranunculus flammula	IV ^{2}	+ ^{2}	II ^{2}	II ^{1}	V ^{2}	III ^{2}
Juncus effusus	I ^{2}	+ ^{3}	I ^{2}	II ^{2}	I ^{1}	I ^{2}
Festuca pratensis	-	+^{1}	+^{1}	+ ^{2}	-	I ^{2}
MOLINIO-ARRHENATHERETEA + FILIPENDULETEA						
Vicia cracca	-	II ^{2}	I ^{2}	III ^{2}	-	II ^{2}
CONVOLVULO-FILIPENDULETEA						
Valeriana officinalis	+^{1}	III ^{2}	I ^{1}	IV ^{2}	-	II ^{2}
Stachys palustris	-	-	-	+^{1}	-	+ ^{2}
Symphytum officinale	+^{1}	-	I ^{1}	I ^{1}	II ^{2}	II ^{1}
FILIPENDULION						
Valeriano Filipenduletum						
Filipendula ulmaria	IV ^{2}	V ^{3}	V ^{4}	V ^{5}	V ^{4}	V ^{6}
Thalictrum flavum	III ^{1}	III ^{2}	III ^{2}	IV ^{3}	V ^{1}	V ^{2}
calamagrostietosum						
Lysimachia vulgaris	IV ^{2}	IV ^{2}	II ^{2}	V ^{2}	V ^{4}	V ^{3}
Calamagrostis canescens	I ^{3}	+ ^{2}	I ^{2}	II ^{2}	III ^{2}	IV ^{4}
Lathyrus palustris	I ^{1}	+ ^{2}	II ^{2}	III ^{2}	V ^{2}	IV ^{2}
PARVOCARICETEA						
CARICION NIGRAE alliance **Caricetum trinervi-nigrae**						
Eriophorum angustifolium	IV ^{3}	I ^{3}	I ^{2}	+^{1}	IV ^{3}	I ^{2}
Agrostis canina	V ^{3}	V ^{2}	V ^{4}	V ^{4}	V ^{4}	V ^{4}
Ranunculus flammula	IV ^{2}	+ ^{2}	II ^{2}	II ^{1}	V ^{2}	III ^{2}
Carex nigra	III ^{3}	IV ^{3}	III ^{2}	III ^{3}	IV ^{3}	III ^{3}
Hydrocotyle vulgaris	II ^{3}	+^{1}	+ ^{2}	+^{5}	I ^{6}	+^{5}
Juncus articulatus	II ^{2}	+ ^{2}	I ^{2}	-	I ^{2}	I ^{2}
Pedicularis palustris	I ^{1}	-	-	-	IV ^{1}	I ^{1}
Potentilla palustris	+ ^{3}	-	-	-	II ^{1}	-
Stellaria palustris	-	-	-	-	-	II ^{1}
Viola palustris	+ ^{6}	-	-	-	-	-
differentiating species with respect to **Agrostietum caninae**						
Carex nigra	III ^{3}	IV ^{3}	III ^{2}	III ^{3}	IV ^{3}	III ^{3}
Stellaria palustris	-	-	-	-	-	II ^{1}
Eriophorum angustifolium	IV ^{3}	I ^{3}	I ^{2}	+^{1}	IV ^{3}	I ^{2}

APPENDIX continued

Plant community	**4**	**1**	**2**	**5**	**6**	**3**
Agrostis canina	V ^{3}	V ^{2}	V ^{4}	V ^{4}	V ^{4}	V ^{4}
Caltha palustris subsp. p	I ^{2}	-	I ^{2}	I ^{2}	III ^{2}	IV ^{4}
Equisetum palustre	V ^{2}	IV ^{2}	V ^{2}	IV ^{2}	IV ^{1}	V ^{2}
CARICION DAVALLIANAE						
Carex oederi s.l.	II ^{2}	-	I ^{2}	-	III ^{2}	-
Carex lasiocarpa	I ^{2}	-	-	-	III ^{4}	-
PHRAGMITION AUSTRALIS						
Phragmites australis	III ^{2}	III ^{2}	IV ^{2}	IV ^{2}	I ^{1}	III ^{2}
Myosotis palustris	$+^{2}$	-	I ^{1}	I ^{2}	-	II ^{2}
Senecio paludosus	$+^{2}$	-	-	I ^{1}	I ^{1}	III ^{2}
CARICION GRACILIS						
Carex acuta	II ^{3}	I ^{3}	II ^{3}	III ^{2}	V ^{4}	V ^{5}
optimum in **CARICION GRACILIS**						
Iris pseudacorus	$+^{1}$	-	-	I ^{1}	I ^{1}	I ^{2}
Phalaris arundinacea	$+^{2}$	$+^{1}$	$+^{2}$	-	-	II ^{2}
Carex disticha	II ^{3}	I ^{2}	I ^{3}	III ^{3}	III ^{2}	IV ^{3}
Galium palustre	III ^{3}	III ^{3}	III ^{3}	III ^{3}	IV ^{3}	III ^{3}
Calamagrostis canescens	I ^{3}	$+^{2}$	I ^{2}	II ^{2}	III ^{2}	IV ^{4}
Lysimachia vulgaris	IV ^{2}	IV ^{2}	II ^{2}	V ^{2}	V ^{4}	V ^{3}
CARICION ELATAE						
optimum in **CARICION ELATAE**						
Galium palustre	III ^{3}	III ^{3}	III ^{3}	III ^{3}	IV ^{3}	III ^{3}
Lysimachia vulgaris	IV ^{2}	IV ^{2}	II ^{2}	V ^{2}	V ^{4}	V ^{3}
Calamagrostis canescens	I ^{3}	$+^{2}$	I ^{2}	II ^{2}	III ^{2}	IV ^{4}

3

Nutrient limitation and nutrient-driven shifts in plant species composition in a species-rich fen meadow

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flooding of the fen meadow

Summary

Nutrient pulses may change the above ground biomass and the plant species composition of species-rich fen ecosystems for years. To investigate the development of these changes we have conducted a single pulse fertilization experiment in a factorial design with N and P, on an undrained and a drained site in a species-rich fen meadow (*Cirsio dissecti-Molinietum*). We monitored biomass production and species composition during four years.

At the undrained site, N fertilization boosted total biomass production, but only in the first year. No N-induced shift was observed in species composition. P fertilization brought about an increase in biomass and a change in species composition from a vegetation dominated by *Carex panicea* to a grassland community with abundant *Holcus lanatus*, but not before the second year. At the drained site, N fertilization had no effect, while P fertilization only resulted in a shift in species composition similar to that observed at the undrained site. At both sites the P induced shift in species composition persisted for four years although the P effect declined during the experiment.

We infer that the decrease of the stress-tolerant *C. panicea* might be a consequence of the increase of more competitive species, like *H. lanatus*. The fast decline of the N effect on biomass production after the first year is probably due to increased denitrification and removal of biomass for hay-making. The delay in the P-effect on biomass and species composition and the persistence of the effect on species composition are ascribed to fast immobilisation and subsequent slow release of fertiliser P in the peat soil. The decline in P-effect on biomass after the second year is ascribed to biomass removal.

The results show that temporary high pulses of P supply, as in a year with frequent flooding, may lead to long-term shifts in species composition without changing total biomass of fen meadows.

Introduction

Eutrophication has had severe impacts on the plant species diversity in fen meadow ecosystems in The Netherlands. As in many other countries in Europe the eutrophication may come from external sources, e.g. increased atmospheric N deposition (up to 60 kg N $ha^{-1}y^{-1}$; Bobbink et al. 1998) and the inflow of agricultural eutrophicated water (up to 47 kg N $ha^{-1}y^{-1}$; Hefting et al. 2003). Eutrophication may also be brought about indirectly: for example, wetland drainage may boost net nutrient release in the soil (Bridgham et al. 1998) and flooding and waterlogging with sulphate-enriched water will stimulate mobilisation of extra phosphate and ammonium (so-called internal eutrophication (Lamers 2001).

Whatever the cause, eutrophication of wet ecosystems increases biomass production and brings about a shift in species composition of the vegetation by stimulating the growth of tall species (Joyce 2001; Bollens et al. 2001). As a consequence of these influences, undisturbed fen meadows hardly exist. In the near future, fen meadows along the upper reach of rivers and brooks, even in nature reserves, will be confronted more frequently by pulses of eutrophication (both external and internal) caused by incidental flooding.

The general question of our study is, whether incidental nutrient pulses in fen meadows will result in a permanently increased biomass production and a consequent shift in species composition.

We conducted a factorial single-pulse N- and P-fertilization experiment in two sites of a *Cirsio-dissecti Molinietum* plant community, situated in the centre and in the margin of a nature reserve, respectively. Airborne nitrogen was influencing the vegetation of the whole nature reserve, while influences from the surrounding farmland (e.g. drainage) mainly affected the margins (Van der Hoek & Van der Schaaf 1988).

The experiment was designed to answer the following questions:

1. Do nitrogen and/or phosphorus limit total aboveground biomass production in the centre and the margin of the nature reserve?

2. Will the species composition of the *Cirsio-dissecti Molinietum* vegetation at these sites change as result of a pulsed increase in N- or P-supply?

3. How long is the time lag between pulse fertilization and the response in biomass production and species composition at these sites and how long will these effects last?

Fertilization experiments are the most straightforward methods to detect nutrient limitation, also in fens (Wassen et al. 1995). Fertilization experiments in fens usually entail adding nutrients once or repeatedly and observing the direct effects only (Verhoeven & Schmitz 1991; Olde Venterink 2000), avoiding that indirect effects of a non-limiting nutrient influence results. To indicate how long a sudden change in nutrient supply will affect an ecosystem we need longer-term experiments, in which also indirect effects have time to develop (e.g. Chapin et al. 1995; Inouye & Tilman 1995; John & Turkington 1997). Only few longer-term experimental fertilization studies investigating the recovery of the vegetation after a single fertilization pulse in fens have been conducted until now (Boeye et al. 1997; Güsewell et al. 2002).

To get insight into the effects of such perturbation and the response time of the community, we applied fertilization in one growing season and observed the effects over four years. We expected that the difference in time-dependence of the effects of N and P might be caused by: (1) longer retention of P than of N in the ecosystem; (2) positive effect of P-fertilization on the availability of N; (3) nutrient export through the repeated harvest of above-ground biomass; (4) changes in species composition.

Material and methods

Site characteristics

The nature reserve "De Bennekomse Meent" (52° 01' N, 5° 36' E) harbours a species-rich, fen meadow at a nutrient-poor soil. The vegetation belongs to the alliance *Junco-Molinion*, association *Cirsio dissecti-Molinietum* (Schaminée et al. 1996). The nature reserve has never been fertilized and has been mown every year in August for centuries. The topography is flat.

In the centre of the reserve the peaty soil is up to 1.5 m thick and upwelling calcareous groundwater reaches the root zone. Here, the most abundant species are *Molinia caerulea* and *Cirsium dissectum* (nomenclature according to Van der Meijden 1990) and small-sedges like *Carex panicea* and *C. hostiana*. Species rare in The Netherlands, e.g. *Carex pulicaris* and *Gentiana pneumonanthe*, also occur frequently in the centre.

The margins of the reserve are a little drained by ditches of neighbouring pastures (Van der Hoek & Van der Schaaf 1988). The peaty O and A horizons extend to a depth of 20 - 50 cm and the influence of calcareous groundwater is less than in the centre. *C. panicea*, *C. hostiana*, *C. dissectum* and *G. pneumonanthe* are less abundant here than in the centre of the reserve, but species such as *Holcus lanatus*, *Plantago lanceolata* and *Filipendula ulmaria* are more abundant.

Table 1: Soil characteristics at the central and the marginal site of the Bennekomse Meent, measured in the top 10 cm soil, one year before the experiment (Van der Hoek & Sykora in prep.). Data are mean values and SE; *n* = number of sampled plots by site. Significant differences between the sites (*t*-test) are indicated: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; n.s.= not significant.

Soil characteristics	**Difference between sites**	**Central site (*n* = 12)**		**Marginal site (*n* = 16)**	
Water level in spring*[1] (cm)	*	7	(2)	12	(2)
Water level in summer*[2] (cm)	***	47	(2)	56	(2)
Moisture content *[3] (%)	**	77	(2)	64	(3)
Organic matter*[3] (kg. m^{-2})	**	14.4	(0.2)	11.5	(0.2)
pH-H_2O*[3]	*	5.72	(0.03)	5.56	(0.06)
pH-KCl*[3]	**	5.24	(0.03)	5.04	(0.05)
Total soil N*[3] (g. m^{-2})	n.s.	493	(20)	450	(19)
Total soil P*[3] (g. m^{-2})	***	17.8	(0.8)	24.1	(1.1)
P-$CaCl_2$*[3] (mg. m^{-2})	*	28.7	(2.2)	46.5	(6.0)
K-$CaCl_2$*[3] (g. m^{-2})	**	3.5	(0.4)	2.3	(0.3)
Net N release*[4] (kg-N.ha^{-1} y^{-1})	n.s.	14.4	(2.6)	10.9	(2.2)

*[1]Below surface; mean of four measurements in one well in spring; *[2]Below surface; mean of three lowest levels in one well in summer; *[3]Sampled at harvest (July); *[4]Net annual N release rate in the top 10 cm soil between May 1988 and May 1991. Release rates are the sum of nine yearly periods, determined from soil incubated in situ.

The soil in the reserve is low in nutrients (Table 1), which is typical for these low productive meadows. Most soil variables differ significantly between the centre and the margins. The soil in the centre is wetter and contains lower total and available amounts of phosphorus. Although the soil of the centre contains more organic matter, the total soil N- and net N- release do not differ significantly. The average extractable K- contents of the soil of both sites agree with published values for small-sedge fen-meadows (Olde Venterink 2000). The extractable K found in the margins was significantly lower than in the centre of the reserve, which is probably due to a greater leaching in the margin (De Mars 1996).

Field experiment

The effects of nitrogen and phosphorus fertilization on biomass production and species composition of the vegetation were investigated on two sites: one in the centre of the reserve and the other in its margins.

At each site, four different fertilization treatments were applied to plots of 1.0 m x 1.2 m in a randomized block design, with five replicates. The four fertilization treatments were: i) no fertilization; ii) nitrogen fertilization (200 kg-N. ha^{-1}, as NH_4NO_3); iii) phosphorus fertilization (40 kg-P. ha^{-1}, as NaH_2PO_4); iv) nitrogen and phosphorus fertilization. These amounts correspond with half the amounts given to pastures if agricultural fertilization recommendations are followed. The amount of nitrogen added was more than twice the sum of N-mineralization (17 kg-N. $ha^{-1}y^{-1}$) and nitrogen deposition (60 kg-N. $ha^{-1}y^{-1}$, Berendse et al. 1994). To obtain an even nutrient distribution over the growing season and to avoid salt damage, nutrients were divided in five equal doses given at three-week intervals, starting on April 17th 1989 and finishing on July 10th 1989. The nitrogen and phosphorus fertilizers (13.7 g NH_4NO_3 and 4.27 g $Na_2H_2PO_4$ per plot respectively) were dissolved in 1 l of demineralized water and carefully sprinkled over the plots. The unfertilized plots received an equal amount of demineralized water.

The resulting response of the vegetation was monitored over four years, until 1992. Each year at the end of July, the vegetation in one subplot (20 cm by 20 cm) within each plot, assigned at random, was clipped to the ground. Vegetation samples were sorted into the following components: *H. lanatus*, *C. panicea*, other graminoids, forbs, mosses, and litter. *H. lanatus* and *C. panicea* are indicative species for a degraded and a typical *Cirsio dissecti-Molinietum*, respectively. The dry weight of the above ground biomass of each component was determined after drying at 70 °C for 48 h. Total N- and P-concentrations in *H. lanatus* and *C. panicea* were measured in the first and second year of the experiment. In the second year we measured also N- and P-concentration in the whole vegetation.

N- and P-concentrations in the biomass were determined colorimetrically, after digesting the dried plant material with H_2SO_4, salicylic acid, H_2O_2 and selenium (Walinga et al. 1995). The K-concentration in the biomass was determined with flame emission spectrophotometry.

Data analysis

The effect of N- and P-fertilization in the field was first analysed using repeated measures analysis of variance (ANOVAR), with N- and P-supply as independent factors and year as the within-subject factor. In addition, a two-way analysis of variance (ANOVA) for each year was performed, as the interaction between year and treatment was often significant. Tukey's post-hoc test was used to test the treatment effects within a year. Shifts in plant species composition were assessed by analysis of the share in total biomass (biomass fractions) of the components. All computations, including the Bonferroni-correction, were done for the total biomass of the clipped aboveground vegetation samples and for the biomass of the selected components, as well as for the square-root transformed biomass fractions of these groups. In order to achieve homogeneous variances, biomass data for some components were ln-transformed. SPSS for Windows (8.0) was used for these calculations.

Results

Biomass and species composition

Central site

At the **central site**, the effect of N-fertilization on (above-ground) biomass production of the vegetation was only visible in the first growing season: the total biomass in the N-fertilized plots was significantly higher than in the controls (Fig. 1). This increased biomass was mainly caused by a significant positive effect of N-fertilization on the biomass of *C. panicea* (Fig. 2). However, there were no effects on the relative contributions of the components to the total biomass (Table 2, below). During the next three years the response to N-fertilization of the biomass disappeared but there was a negative nitrogen effect on litter in the last year (Fig. 2).

During the first growing season P-fertilization did not bring about a higher total (above-ground) biomass. A positive effect of P-addition on total biomass was only measured in the second growing season (Fig. 1). The higher total biomass was caused by an increase of the biomass of *H. lanatus*, other graminoids (except *C. panicea*) and litter (Fig. 2). This resulted in an increased contribution of *H. lanatus* at the cost of *C. panicea* (Fig. 2; Table 2). In the fourth year there was still a significantly increased biomass of *H. lanatus* in the P-fertilized plots (Fig. 2; Table 2).

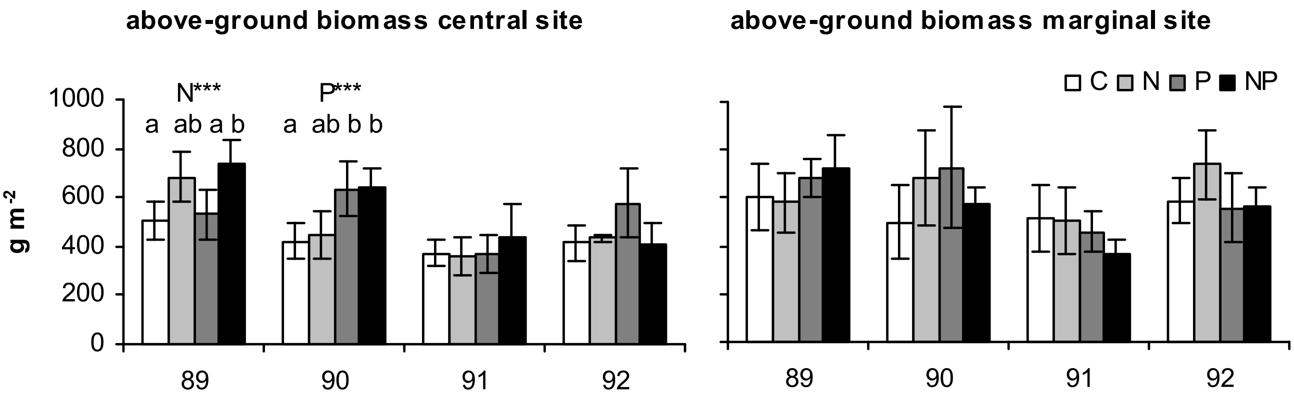

Figure 1: Above-ground biomass of the vegetation at the central and marginal site of the Bennekomse Meent during four growing seasons after N-and P-addition in the first year. Bars are means ± SE (five replicates). Significant treatment effects for each year are indicated. Level of significance: *** = $p < 0.001$. Bars sharing a letter are not significantly different within a year and the outcome is shown only if significant treatment difference was observed (at $\alpha = 0.05$, Tukey's post-hoc test).

Marginal site

At the **marginal site**, the total above ground biomass of the vegetation of the control plots was significantly higher than at the central site (ANOVAR, $p < 0.05$). The difference in total biomass between both sites was largely controlled by the forbs and graminoids, but not by *C. panicea*. Neither the N- nor the P-supply affected total biomass production in the first and subsequent years (Fig. 1). There was no significant N-effect on the biomass of the components in the first year (Fig. 2). As at the central site N, fertilization did not induce major changes in species composition (Table 2).

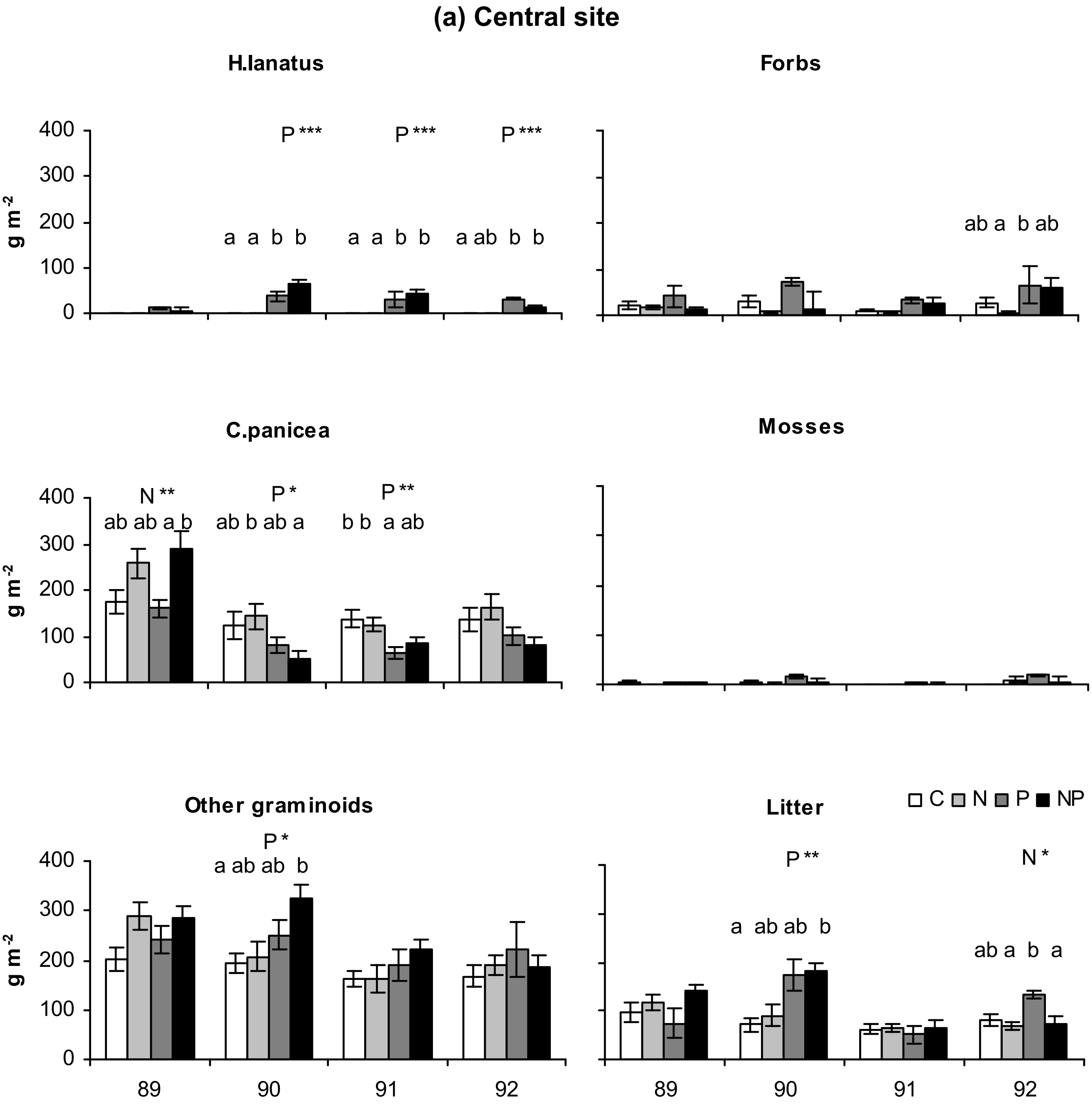

Figure 2 continued:

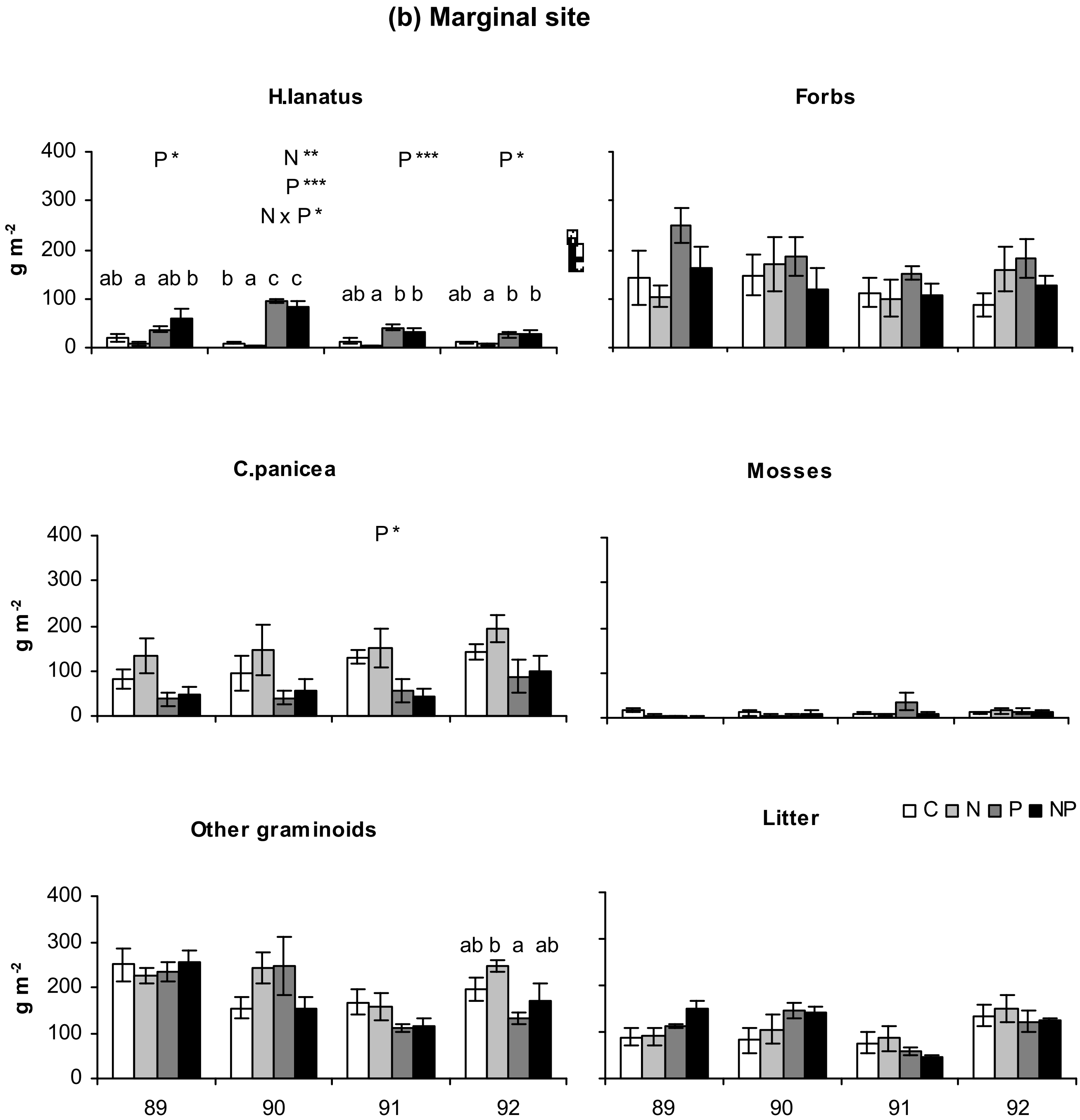

Figure 2: Above-ground biomass of *Holcus lanatus*, *Carex panicea*, other graminoids, forbs, mosses and litter at the central **(a)** and marginal site **(b)** during 4 years after N- and P-addition in year 1. Bars are means ± SE (five replicates). Significant treatment effects for each season are indicated; * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ (2 x 2 ANOVA). Bars sharing a letter are not significantly different within a year and the outcome is shown only if significant treatment difference was observed (at α = 0.05, Tukey's post-hoc test).

Although P-addition did not change total biomass, it increased the biomass of *H. lanatus*, whereas the biomass of *C. panicea* decreased. The P-effect on biomass of *H. lanatus* was significant for four years (Fig. 2) and ANOVAR showed a negative overall effect of P on biomass of *C. panicea* ($p < 0.05$). Accordingly, in the P-fertilized plots the biomass fraction of *C. panicea* was lower and that of *H. lanatus* and litter increased in the first year (Table 2). This shift in species composition slowed down over time. By the end of the fourth year, the increase of the biomass fraction of *H. lanatus* in P-fertilized plots still existed (Table 2; ANOVAR, $p < 0.001$).

Table 2: Results of an ANOVA with N- and P-addition as factors and biomass fractions of *Holcus lanatus*, *Carex panicea*, other graminoids, forbs, mosses and litter as plant variables at the central and marginal site. *F*- values with their levels of significance ($^{+}$ = $p < 0.05$, $^{++}$ = $p < 0.01$, $^{+++}$ = $p < 0.001$). *df*- treatment: 1 and *df* -total: 20. Only significant effects are presented. No significant effects of N and N x P interaction were found.

Sites / components	**P-effects**			
	Year 1	**Year 2**	**Year 3**	**Year 4**
Central site				
Holcus lanatus		166.7^{+++}	50.8^{+++}	107.9^{+++}
Carex panicea		26.3^{---}	30.5^{---}	
Other graminoids				
Forbs			10.0^{+}	
Mosses				
Litter		10.2^{+}		
Marginal site				
Holcus lanatus	10.6^{++}	319.5^{+++}	83.7^{+++}	17.3^{++}
Carex panicea	11.5^{-}			
Other graminoids				
Forbs			9.7^{+}	
Mosses	9.7^{-}			
Litter	7.5^{++}	12.0^{+}		

N and P concentrations in the plant biomass

At the **central site**, N-fertilization increased the N-concentration in *C. panicea* in the first year (Fig. 3). ANOVAR showed a positive overall N-effect on P-concentrations in *C. panicea* in the first two years of the experiment (p < 0.05). P addition led to significantly increased P concentrations in total vegetation (1990) and to increased N and P concentration in *C. panicea* in both years (Fig. 3).

At the **marginal site**, the N- and P-concentrations in the total vegetation of the control plots were significantly higher than at the central site ($p < 0.05$ and $p < 0.10$, respectively), largely because of the significantly higher concentrations in *C. panicea* and *H. lanatus*. The scarcity of *H. lanatus* in the control plots of the central site prevented us from carrying out a full analysis. N-fertilization increased the N-concentration in both species in the first year (Fig. 3).

P-addition increased the P-concentration in the total vegetation. It is notable that the significant positive P-effect on the P-concentration of *C. panicea* occurred in the marginal site only in the second year.

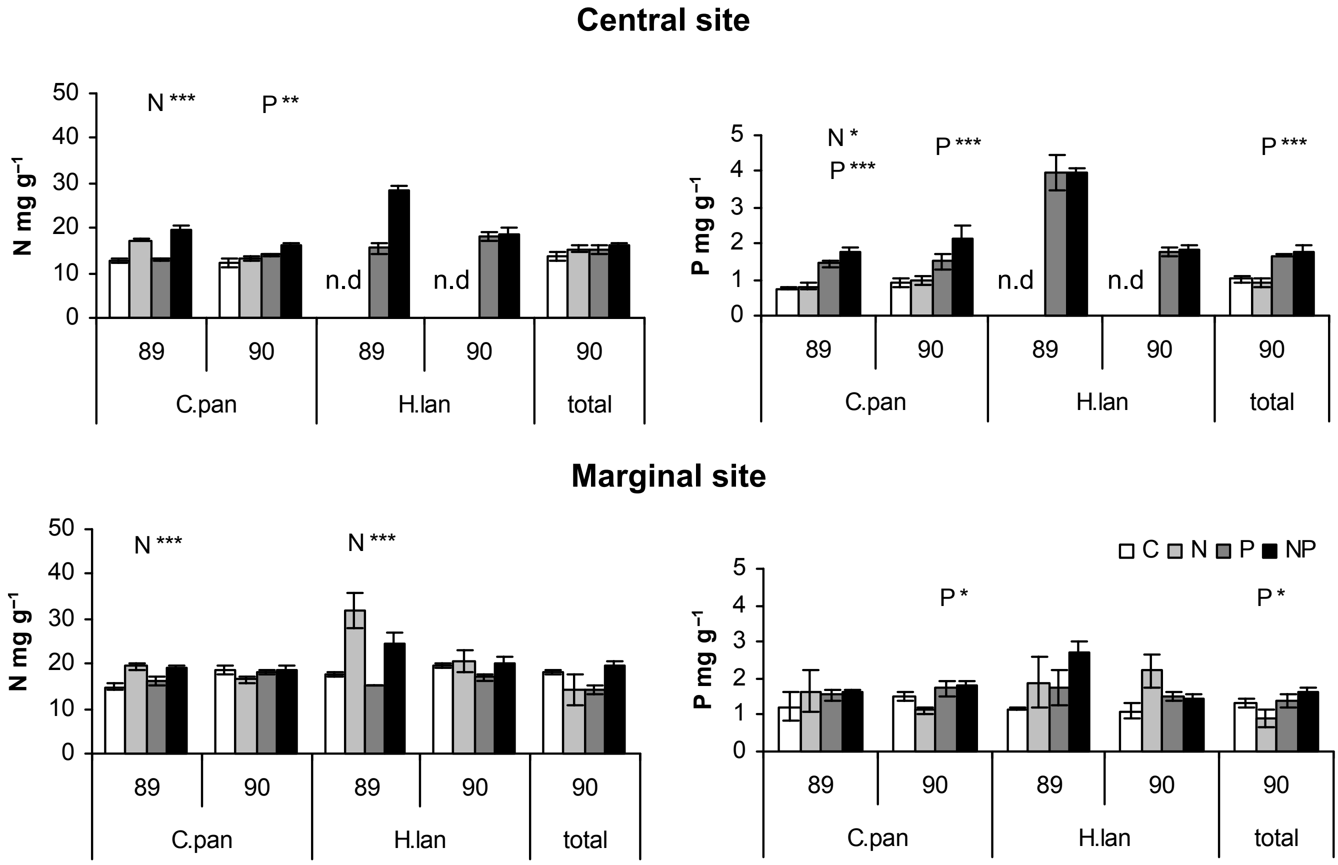

Figure 3: N- and P-concentrations in *Holcus lanatus*, *Carex panicea* in the first and second year after N- and P-addition on the central and marginal site. Concentrations in the total vegetation in 1990 are also presented. Bars are means ± SE (five replicates). Significant treatment effects for the first and second season are indicated. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ (2 x 2 ANOVA). n.d. = no data

Discussion

Our first question was which nutrient limited total above-ground biomass production in the investigated sites. From the effect of N- and P-addition in the first and second year respectively, we conclude that nitrogen and subsequently phosphorus were limiting plant growth of the wet *Cirsio dissecti-Molinietum* vegetation at the central site. This finding is in agreement with the results of Olde Venterink et al. (2001) and Van Duren et al. (1997) who found that N is the limiting nutrient for biomass production in small-sedge meadows. Taking into account the effect of P-addition in the second year we could have concluded that N and P were co-limiting biomass production of the vegetation.

At the marginal site, neither N nor P limit the growth of the total vegetation which is in accordance with Olde Venterink et al. (2001). The slightly higher fertility of the margin site – e.g. more available P in the soil (Table 1) and probably a higher N-release in spring (Van der Hoek & Braakhekke 1998) – may explain that N- and P-concentration in the total vegetation of the control plots were significantly higher than at the central site. The increase in P-concentration in the biomass upon P-addition shows that biomass production at the marginal site is not limited by the nutrients we supplied. Instead K may be limiting, which is also indicated by the low K concentration in the plant material (ca. 3.5 mg g^{-1}) and the K:P and the N:K ratios compared to the critical values given by Pegtel et al. (1996). Leaching may be responsible for the low extractable K in soil especially in the drained marginal site (De Mars 1996).

Our second question concerned the change in species composition of the vegetation as result of N-and P-fertilization. N-fertilization had no major effects on species dominance. *Carex panicea* benefited from N-fertilization, but its share in total biomass was not significantly affected. P-fertilization did result in a change in species composition at both sites: the fraction of *H. lanatus* biomass increased at the cost of *C. panicea.* Our general conclusion is that the growth of the most responsive species *C. panicea* and *H. lanatus* was actually limited by N and P, respectively. *C. panicea*, being a slow growing and stress-tolerant species (Grime et al. 1988), is well equipped to take up P and is not hampered by a low P-supply (Boeye et al. 1999). It responded to increased P-availability by increasing the P-concentration in its tissue, which is typical of stress-tolerant species (Chapin 1980). Pauli et al. (2002) and Theodose & Bowman (1997) also found that the biomass of *Carex* species responded particularly positively to addition of nitrogen.

The absence of any effect of the P-stimulated growth of *H. lanatus* on species composition at the central site in the first year was caused by its very low initial cover, although we observed an increased growth in the autumn of the first year. *H. lanatus* has profited in the P-treatments during the second year. We infer that the decrease of *C. panicea* has been a consequence of the increase of other species, among which *H. lanatus*. Pauli et al. (2002) and Pegtel (1983) also concluded that an increase in P supply leads to a shift in species composition in favour of grasses and at the cost of *Carex* species.

We found in our experiment that P-fertilization may indeed change the species composition without a preceding or concurrent increase of biomass. From the absence of biomass increase, we infer that the found shift in species composition is not caused by increased competititon for light, the more so as even a P-effect on the biomass of mosses did not occur.

Our third question concerned the time lag between N-and P-fertilization and the response in biomass production and species composition and the persistence of these effects. The positive effect of N-fertilization on total above-ground biomass at the central site disappeared already one year after application, mainly as a consequence of the disappearance of the positive response of *C. panicea*. The increase in the biomass of *H. lanatus* and of other graminoids (except *C. panicea*) after P-fertilization occurred relatively late, which explains that the positive effect on total above-ground biomass was not observed till the second growing season.

The shift in species composition, an increase of *H. lanatus* at the cost of *C. panicea*, caused by P-fertilization faded away gradually after the second year. Although, even in the fourth year *H. lanatus* had still a higher biomass. Boeye et al. (1999), also found that competitive species scored still higher in the fertilized plots at the expense of stress tolerant plants in the fourth year after application in a degraded *Cirsio dissecti-Molinietum*.

The disappearance of the effects of N-supply in the central site already after the first year might be caused by the removal of the supplied N by hay-making, the N-output by denitrification and the storage of N in soil organic matter. Leaching might be negligible as a consequence of the upward seepage of groundwater at this site (Van der Hoek & Van der Schaaf 1988) and we never found a significant N-effect on N-concentration in the groundwater after fertilization. The N input in the control plots is restricted to atmospheric N deposition (60 kg-N.ha^{-1}y^{-1}).

Since the maximal N-output by hay-making from the control plots, removing total standing crop inclusive litter, accounts for ca. 56.5 kg-N.ha^{-1}y^{-1}, we concluded that the sum of the storage of N in soil organic matter and denitrification is small in these plots (3.5 kg-N.ha^{-1}y^{-1}). Hay-making appears to be the important factor to maintain nitrogen-poor conditions in our fen meadow. In the first year we calculated an extra N-removal in the N fertilized plots of 36 kg-N.ha^{-1}. But the extra N removed from these plots by hay-making in the second and fourth year was small (11 and 13 kg-N.ha^{-1} respectively), despite the substantial gift of 200 kg- N.ha^{-1}. We infer that most of the extra N supplied might have disappeared by absorption in the soil and increased denitrification, directly after the addition of N. Half of the N was given as nitrate and the high organic matter content and high groundwater level in spring are favourable to denitrification (Hefting et al. 2003). In unfertilized meadows such as these, the N-output by denitrification is relatively low (17 kg-N.ha^{-1} y^{-1} according to Berendse et al. 1994), but directly after fertilisation losses may be high (for instance 36–42 kg-N.ha^{-1} y^{-1} on grazed fertilized peaty grasslands acc. to Hefting et al. 2003).

In our experiment the effects of P-fertilization lasted longer than the N-effects. Probably most of the added phosphorus, 40 kg ha^{-1}, was soon removed from the soil solution by adsorption to Fe- and Al- oxides and to organic matter and was released only slowly during the subsequent years (Patrick & Khalid 1974; Van der Peijl et al. 2000). In the central site the increased P-release must have been sufficiently large to result in a significant increase of total biomass, but only in the second year. The increased growth of *H. lanatus* in the autumn of the first year together with the significantly increased amount of litter in the second year suggest (acc. to Aerts & de Caluwe 1997 and Güsewell et al. 2002), that the increased P- (and N-) release, necessary for the enhanced plant biomass in the second year, was caused by decomposition of litter of *H. lanatus* especially.

Because decomposition of litter from fast-growing species generally exceeds that from slow-growing species and changed species composition following nutrient input may increase the nutrient release from litter, several authors (Berendse 1999; Strengbom et al. 2001) found that fast growing plants may be able to persist in a community even after the nutrient input has been reduced. Our results suggest such a feed-forward effect driven by *H. lanatus* and the effects of P-release on species composition lingered at both sites up until the fourth year.

The P-output by hay-making plays an important role in the recovery of our fen meadow ecosystem. We found a significant P-fertilizer effect (ANOVA, $p < 0.001$) on the P removed by hay-making in the central site during the second year. The average P-removal was about 8 kg-P.ha^{-1} in the P fertilized plots at both sites that year but decreased later on and corresponded again to the amounts removed from the control plots in the fourth year (about 2 kg-P.ha^{-1} in the centre and 4 kg-P.ha^{-1} in the margin).

The corollary of our investigation is that incidental nutrient pulses, caused by flooding with heavily eutrophicated surface water for example, could lead to long-term changes in species composition of *Cirsio dissecti-Molinietum* plant communities in floodplains, when they repeatedly occur with intervals of 5 yr or even shorter.

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4

Restoration of soil chemical conditions of fen-meadow plant communities by water management in The Netherlands

Van der Hoek D. & Braakhekke, W.G. 1998. In: Joyce C.B. & Wade P.M. (eds.) *European Wet Grasslands: Biodiversity, Management and Restoration*. pp.265-275. Wiley, London, UK.

Summary

The availability of nitrogen (N) and phosphorus (P) in most of the nutrient-poor, species-rich fen-meadow ecosystems in The Netherlands has increased due to lowering of the groundwater level. Consequently biomass production has increased and many species have become locally extinct.

The effects of the availability of N and P on *Cirsio-Molinietum caeruleae* plant communities were studied in fertilizer trials in the centre and on the border of a nature reserve. It is concluded that there was co-limitation by N and P in the relatively wet centre of the reserve, while there was only P limitation on the border where groundwater level had been lowered by drainage. The species composition of these communities appeared to be determined by the inorganic P concentration in the soil solution, which is known to depend on the chemical composition of the soil water, while the biomass production is determined by the annual P flux resulting from turnover of the large pool of organic P, which is known to depend on the groundwater level.

A continuous upward seepage of calcareous groundwater into the root zone is considered to be essential for maintaining the chemical conditions in the root zone and for reducing fluctuations in the groundwater level in the growing season. Hydrological models were used to predict the impact of restoration measures on the quantity and quality of water in the root zone. It is concluded that the characteristic site conditions for a *Cirsio-Molinietum* fen meadow can be restored by reduction of deep drainage in the surroundings of the reserve, for example by partial infilling of ditches, in combination with measures inside the reserve such as the cutting of shallow trenches to remove surplus rainwater and turf-stripping to lower the surface level.

Introduction

Until 50 years ago, nutrient-poor, base-rich fens and fen meadows were common in The Netherlands. Fens comprise minerotrophic wetland vegetation on peaty soils. Fen meadows are semi-natural ecosystems derived from fens by extensive agricultural exploitation for hay-making without fertilization, but with some degree of drainage (Wheeler 1995). One of the typical plant communities in fen meadows is *Cirsio-Molinietum caeruleae* (nomenclature of plant communities follows Westhoff and den Held 1969). This community corresponds to the British National Vegetation Classification community type M24 (Rodwell 1992) and CORINE biotope *Junco-Molinion* 37.312 (Moss et al. 1991). When the agricultural use is intensified by fertilization and deep drainage, a fen meadow develops into a hay meadow with an *Arrhenaterion* or eventually a *Poo-Lolietum* type of vegetation.

Almost everywhere in The Netherlands the relics of oligotrophic fens and fen meadows have become increasingly eutrophicated and acidified. An important factor in this process has been the lowering of groundwater, caused by exploitation of deep groundwater for drinking water and by drainage for agriculture. Lowering of groundwater levels has resulted in an increased availability of nitrogen and phosphorus in the soil. Water infiltrating as precipitation and nitrogen deposition from the air have further contributed to the eutrophication and acidification. Consequently, biomass production in these vegetation types has increased, but as a result many species have become endangered or extinct.

In most fen nature reserves in The Netherlands it is relatively simple to maintain a high groundwater level during the summer, because there is usually a large storage capacity for winter precipitation facilitated by a system of sluices for controlling water level. Experiments with additional fertilizer and studies of nutrient balances in rich-fen quagmires (*Caricion davallianae*, CORINE biotope 54.231; Moss et al. 1991), have shown that nitrogen is the main limiting factor for plant growth. Despite the high rate of nitrogen deposition of 40 kg ha^{-1} yr^{-1}, management by hay-making appears to have been sufficient for the conservation of species-rich plant communities in fens (Verhoeven et al. 1994).

In fen meadows on peaty and sandy soils, the situation is different. Despite hay-cutting management for many years, grasses have become dominant over sedges and herbs in most Dutch fen meadows. Introduction of surface water is no solution, because it is usually too eutrophicated due to over-manuring of the surrounding agricultural land. Special water management is needed to maintain or restore the characteristic abiotic site conditions. It is known that the availabilitity of nitrogen and phosphorus should be low for these wet, nutrient-poor grassland communities.

In this chapter we describe the application of some water-management measures for restoration of the characteristic site conditions for a *Cirsio-Molinietum caeruleae* fen meadow vegetation. We also present results of a study into the effects of groundwater level on the availability of nitrogen and phosphorus in soil and their uptake by the vegetation.

The impact of groundwater on the availability and uptake of nutrients

Kemmers (1986), Grootjans (1985) and others have shown that the depth and quality of the groundwater have important effects on the availability of nitrogen and phosphorus in wet, nutrient-poor grassland communities. To gain insight into these key factors we conducted descriptive and experimental research in *Cirsio-Molinietum* communities in the Bennekomse Meent, a nature reserve near Wageningen, in the centre of The Netherlands (Figure 1). The relationships between groundwater level, groundwater quality, availability and uptake of nitrogen and phosphorus, and species composition of the vegetation, were studied.

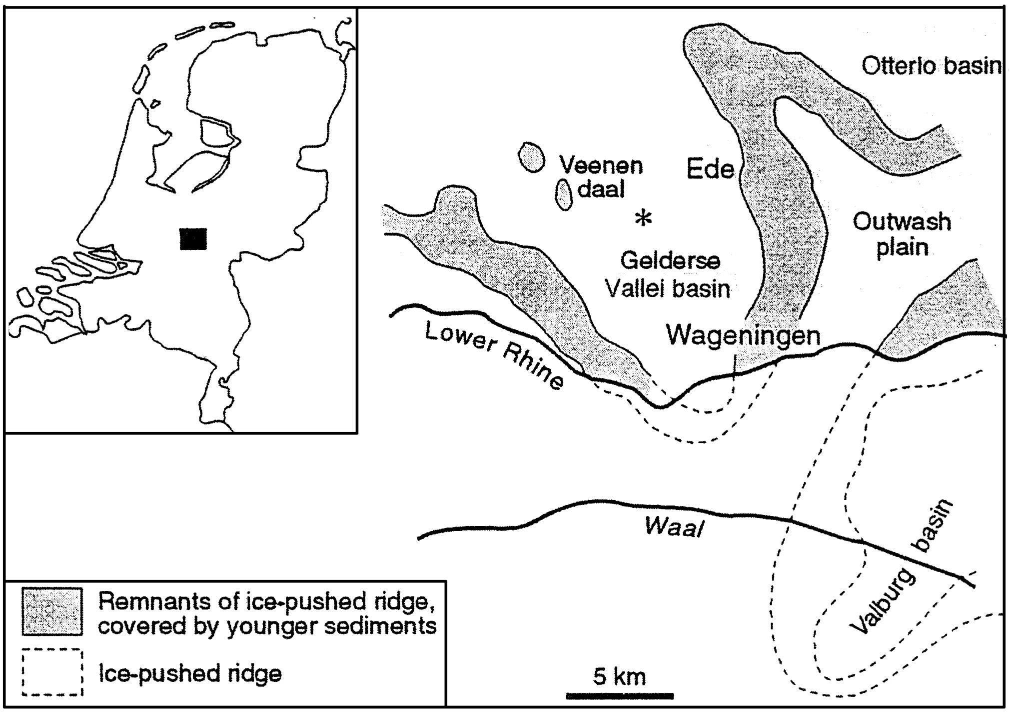

Figure 1. Location of the Bennekomse Meent study area, shown by asterisk, and basins and ridges of the Saale glacial tongues.

Site description

The Bennekomse Meent is a 14-ha remnant of formerly extensive communal hay fields consisting of a number of nutrient-poor, species-rich, fen meadows. It is situated in the centre of a valley, the Gelderse Vallei, a glacial trough enclosed by ice pushed ridges. In the valley fill, two aquifers can be distinguished, separated by less-permeable layers of peat and clay. The groundwater in the deepest aquifer is mainly supplied by the infiltration area in the east. Movement from the middle aquifer towards the upper one is about 0.6 mm.day^{-1} and is generally greater in summer than in winter. The influence of calcareous, vertical seepage water from this artesian aquifer is more or less predominant over precipitation water in the peaty topsoils of the nature reserve.

Nowadays the Bennekomse Meent is protected as a nature reserve surrounded by heavily fertilized agricultural land. The border zones of the reserve are influenced by extra nutrient inputs and drainage (Van der Hoek & Van der Schaaf 1988). Historical data on the species composition of the area show a over the last 50 years, from species that indicate nutrient-poor habitats and calcareous conditions, such as *Carex panicea* and *Carex hostiana*, to fast-growing species that indicate less calcareous and more nutrient-rich conditions, in particular *Holcus lanatus* (nomenclature of plant species follows Tutin et al. 1964-1980 and Heukels & Van der Meyden, 1990). We have studied three sites in this nature reserve in more detail (Figure 2): site A near the east corner of the reserve; site B near the north-east border; and site C in the centre of the reserve, which is the least disturbed site, with the deepest peat layer and the strongest influence of upward seepage.

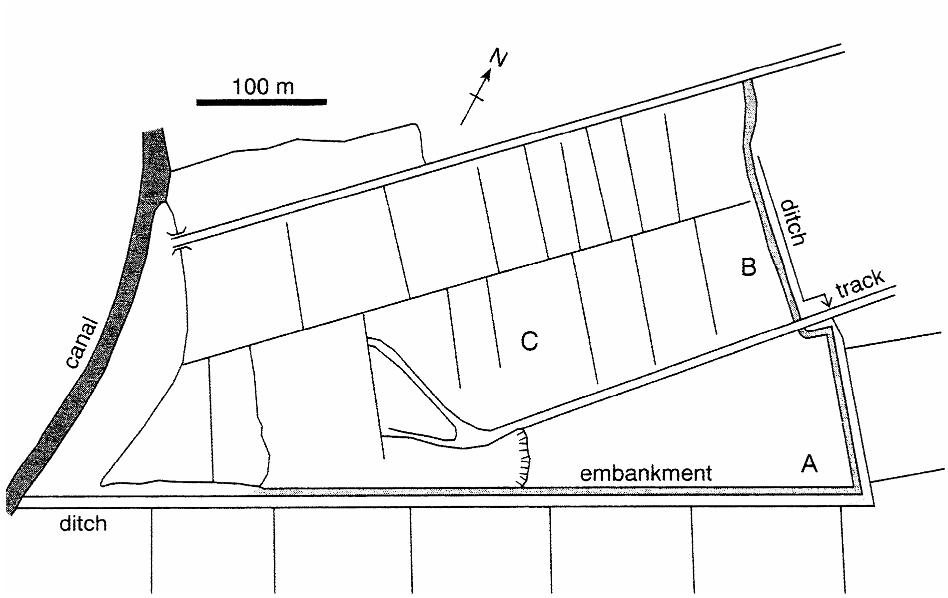

Figure 2. Position of study sites (A, B and C) in the Bennekomse Meent.

Site A has thin peaty soils (about 20-cm thickness) and the groundwater level is influenced by the drainage of the surrounding agricultural area. It has been enclosed by an embankment to accumulate precipition water and reduce desiccation of the vegetation. Species like *Anthoxantum odoratum*, *Danthonia decumbens*, *Festuca rubra* and *F. ovina* have increased here.

Site B has an intermediate position in between site A and C. The peaty topsoil extends down to a depth of 20–50 cm and there is some drainage caused by the border ditch. The influence of calcareous seepage water is stronger than at site A, but less than at site C. *C. panicea*, *C. hostiana*, *Cirsium dissectum* and *Gentiana pneumonanthe* are decreasing at site B, while species like *Holcus lanatus*, *Plantago lanceolata* and *Filipendula ulmaria* are increasing.

Site C has peaty soils up to 1.5 m thick and calcareous seepage water reaches into the root zone. The most abundant species are *C. panicea*, *C. hostiana*, *Molinia caerulea* and *C. dissectum*. Rare species like *Carex pulicaris*, *G. pneumonanthe* are abundant. During the last 50 years, there has been no notable shift in species composition or dominance at this site.

Fertilization experiment

To investigate which element is limiting in the centre and border zone (at sites C and site B) a 2 x 2 factorial fertilization experiment was carried out, in which, for a period of one year, nitrogen (N) was applied at rates of 0 and 200 kg N ha^{-1} and phosphorus (P) at rates of 0 and 40 kg P ha^{-1} (Van der Hoek et al. in prep.). The rates were calculated to be sufficiently high to eliminate any limitations and were based on soil conditions and previous experiments. The response of the vegetation was monitored over four years.

At site C, N fertilization resulted in increased biomass production, but no shift in the relative contributions of different groups of species was observed. P fertilization did not result in increased biomass production, but did cause a shift in botanical composition, from a sedge-dominated vegetation, with high abundance of *C. panicea*, towards a grass-dominated vegetation with high abundance of *H. lanatus*. This shift started only in the second year after P fertilization. At site B, N and P fertilization had no effect on above ground biomass, while P fertilization resulted in a shift in vegetation composition similar to that in site C.

The lack of response of the biomass production to N fertilization at site B shows that N availability was not limiting at this site, probably because of extra N input from the adjacent pasture or from high N mineralization rates in spring when the ground water level is dropping. In contrast, at site C, the increase in biomass production after N fertilization shows that N was limiting growth.

The lack of response of the biomass production at site C to application of P does not disprove that P availability is a limiting factor. Since P is easily adsorbed to the soil it is possible that the applied P rates were insufficient to saturate the capacity of the soil to fix P. Even though biomass production was not increased, P application did change the species composition of the vegetation. Therefore it is concluded that P supply was limiting growth at both sites, which means that there was co-limitation by N and P at site C, which supports the most typical *Cirsio-Molinietum* community. The *Cirsio-Molinietum* community could have been derived from a *Caricion davallianae* community by selective P depletion due to long-continued mowing management, resulting in biomass production and species composition that are probably equally or even more limited by P availability than by N (Verhoeven et al. 1994).

It is possible that the species composition at site C changed whilst the biomass production did not increase, because, although most of the added P was fixed, the equilibrium P concentration in the soil solution was increased just enough for the less P-efficient and more P-demanding species to benefit, but not enough to increase total biomass production. This would imply that biomass production in these *Cirsio-Molinietum* communities is mainly determined by the annual P flux that results from decomposition of organic matter, while the species composition is mainly determined by the P-concentration in the soil solution, which is in turn determined by the exchange equilibrium with the P adsorbed to the soil. The quality of the water in the root zone (pH and concentrations of Ca^{2+}, Fe^{2+} and Al^{3+} ions) may regulate the P concentration, while water quantity, especially the groundwater level, may regulate the P flux.

Availability of nitrogen and phosphorus at *Cirsio-Molinietum* sites

To test the above hypotheses, we studied several processes that determine the availability of N and P in soil and their uptake by the vegetation at 44 plots evenly distributed over the sites A, B and C. Depth of the groundwater table was measured twice a month at each site. Mineralization of N was measured over a period of three years, by means of in situ incubation of undisturbed soil cores at 0–15 cm depth (according to Raison et al. 1987). In soil samples the following variables were measured: pH(H_2O), pH(KCl), percentage organic matter, P fractions (total P, soluble P, P-FeOOH, P-$CaCO_3$, organic P; according to de Groot and Golterman 1990). During the growing season in 1994, the vegetation was sampled five times; biomass and mineral content were measured.

A positive correlation between depth of groundwater table and nitrification of the plots was found at the *Cirsio-Molinietum* sites A, B and C. The fluctuations during the growing season are illustrated in Figure 3.

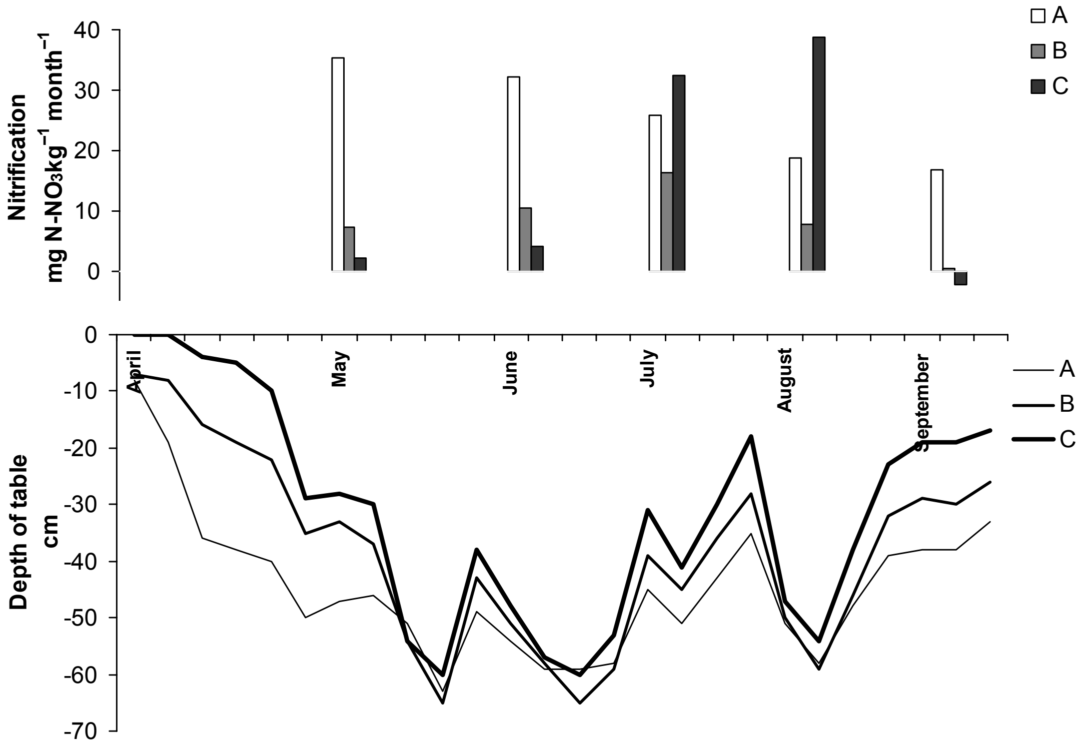

Figure 3. Groundwater depth (cm below surface) and net nitrification (mg N-NO_3^- kg dry soil^{-1} month^{-1}) at three hydrologically different sites (study sites A, B and C) of a *Cirsio-Molinietum* ecosystem.

At site C, high groundwater levels (up to the soil surface) retarded nitrification at the beginning of the growing season. However, as a consequence of the high percentage of organic matter (56 %) and the low water table in summer, annual nitrification may still have been considerable. At sites A and B, water levels started to fall earlier, leading to stronger nitrification in spring. These results are in accordance with Grootjans (1985), who stated that site conditions of *Cirsio-Molinietum* communities are characterized by temporary inundation, high water tables in spring and a maximum groundwater depth of approximately 60 cm below surface in summer. Koerselman & Verhoeven (1995) have shown that a change in the trophic status of fens cannot always be explained by external inputs. It may also result from a change in the rates of soil nutrient release, associated with changed environmental conditions, such as a lowering of the water table. This 'internal eutrophication' can be very important, particularly in older successional stages with large organically and chemically complexed nutrient pools in the soil.

Where upward seepage has been reduced, storage of precipitation water by means of an embankment (as in site A) is not effective in restoring the required groundwater levels. In spite of the embankment, the groundwater level at site A falls relatively rapidly in early spring due to drainage. Moreover, conservation of rainwater is deleterious to groundwater quality. In the topsoil of the enclosed site A, rainwater had a considerable influence as evidenced by a relatively low pH and a high content of sulphate. At site C, which is not embanked, higher pH values and a dominance of Ca^{2+} and HCO_3^- ions occurred in the rootzone, caused by the influence of the upward seepage of calcareous groundwater (Van der Hoek & Van der Schaaf 1988).

The soil processes affecting the availability of P are complex. Using information provided in Bolt & Bruggenwert (1978), we constructed a conceptual diagram of P flow, which consisted of pools and fluxes, emphasizing the role of P in the soil solution (Figure 4). The pool sizes and rates were based on the results of the investigation. They represent an average of the three sites A, B and C. In constructing Figure 4 it was inferred that, at these *Cirsio-Molinietum* sites, the decomposition of soil organic matter (specific rate of P mineralization x the amount of organic matter) determines the net flux of phosphate to the soil solution and that the concentration of phosphate in soil solution is regulated by sorption processes in combination with an efficient uptake by the vegetation, as hypothesized above.

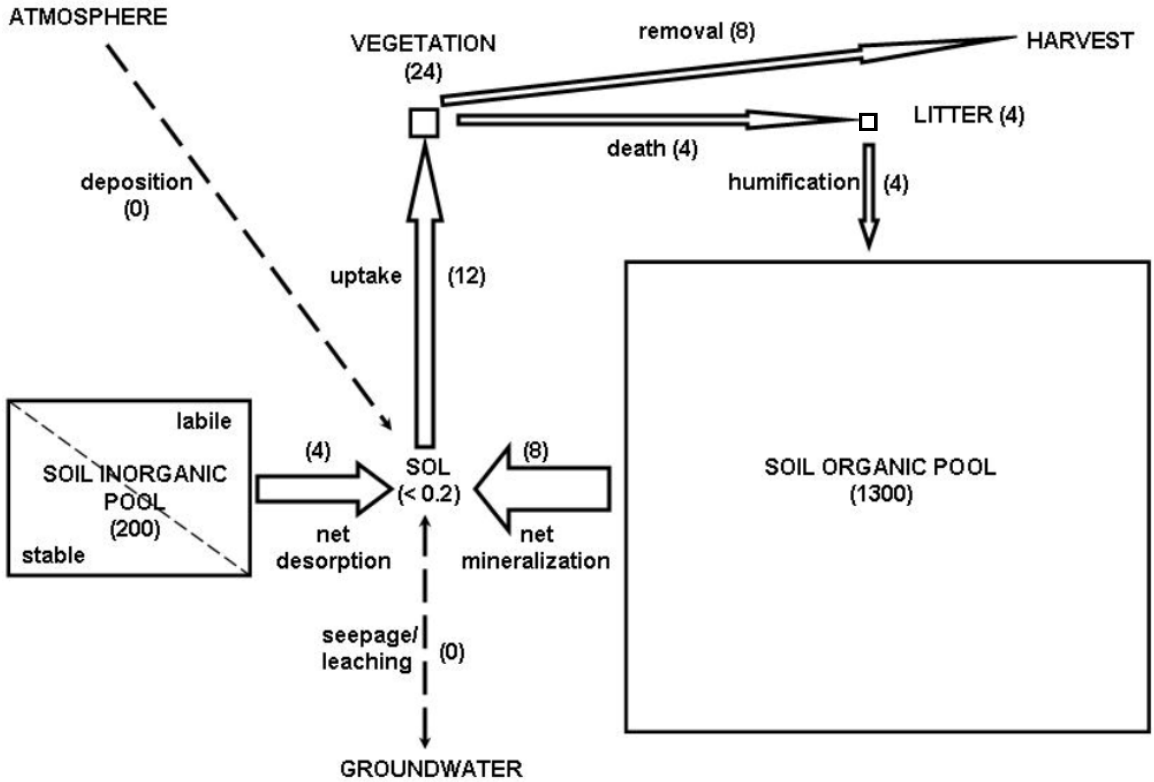

Figure 4. Phosphoros (P) flows (kg ha^{-1} yr^{-1}) and P pools (kg ha^{-1}) in a *Cirsio-Molinietum* ecosystem at a maximum depth of 20 cm.

The total amount of phosphate in the topsoil (0–20cm) appeared to be about 100 times as high as the amount present in maximum standing crop and litter. Figure 4 shows that this is mainly organic P. The turnover rate of this pool is very slow. Since there is also a prominent pool of inorganic P, desorption of labile, inorganic P can also be important for the supply of phosphate to plants, especially under changing soil chemical conditions. Desorption of P will proceed much faster than P mineralization, but will eventually lead to a new dynamic equilibrium with a negligible annual net P desorption.

It is concluded from the available data that a change in solubility of P compounds (P-FeOOH and P-$CaCO_3$) due to changes in soil pH has not been a key factor in determining the changes in availability of P in the Bennekomse Meent. This is because at all *Cirsio-Molinietum* sites the pH appeared to be buffered at about 5.5 by cation exchange of the adsorption complex in soil. The presence of calcareous groundwater in the rootzone is a prerequisite to maintain this buffer capacity. Consequently changes in N availability were considered to be the main cause of changes in vegetation composition in the border sites A and B.

Uptake of N and P by *Cirsio-Molinietum* communities

The uptake of N and P by *Cirsio-Molinietum* communities differed considerably between the investigated sites, especially at the beginning of the growing season. This was expressed in the concentration in the plants (Figure 5) as well as in the uptake of N and P m^{-2} yr^{-1} (not shown). In May, the N concentration of plant material at site A exceeded that at site B and the concentration at site B was greater than at site C. Based on data for the whole growing season as well as just May, the P concentration in plant material also differed between the sites. The P concentration of plant material at site C was less than at sites A and B.

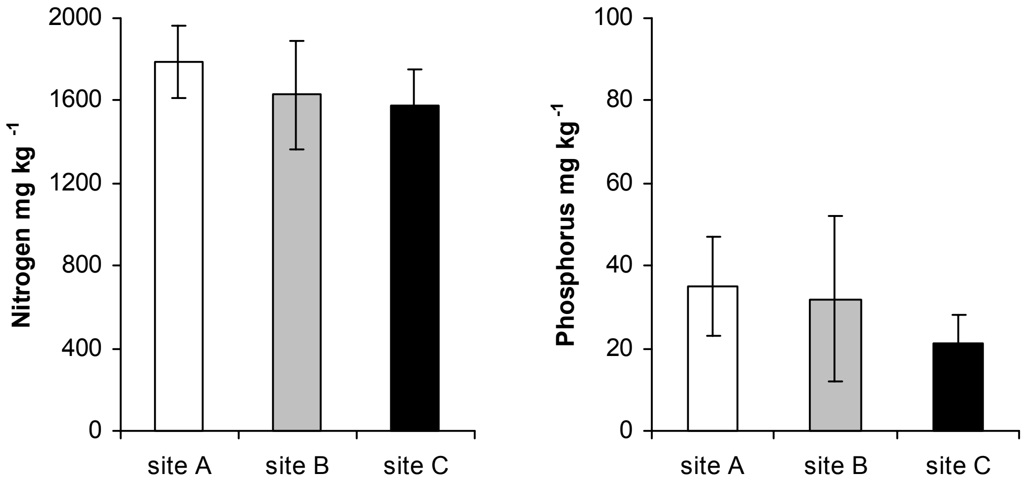

Figure 5. Concentration of nirogen (N) and phosphoros (P) in above-ground biomass of the total vegetation at the *Cirsio-Molinietum* study sites A, B and C in May 1994. The error bars indicate ± 1 SE.

N : P ratios in plant material, measured in July for each of the three years, were relatively low at all three sites. The mean N : P ratio at sites A and B fluctuated from 12 to 19, while the values were somewhat higher (13–22) at site C, caused by a low P concentration in spring. Pegtel et al. (1996) and Koerselman & Verhoeven (1995) showed that production of biomass of plant communities is limited by P when the N:P ratio in the biomass is higher than 11 and 16 respectively. These data indicate that, at all sites of *Cirsio-Molinietum* investigated, biomass production is limited by P availability. Moreover the results of the fertilizer experiment showed a co-limitation of N and P at site C.

The main conclusion of these investigations is that continuous upward seepage of calcareous groundwater in the rootzone is essential for the maintenance of two conditions that are typical for *Cirsio-Molinietum* communities: a high buffer capacity in the root zone and high groundwater levels in spring and summer, ensuring a low mineralization of N and P. Moreover, high water levels restrict the depth of rooting, leading to greater competition between plant species and a lower nutrient uptake per m^2 (Aber & Melillo 1991). Deep-rooting species, like many grasses, are hampered and shallow-rooting, stress-tolerant species, like the sedges, are favoured under these wet and nutrient-poor conditions.

Effectiveness of water management for restoration

Restoration of site conditions for *Cirsio-Molinietum* communities requires a combination of measures. First, measures have to be taken to decrease losses of water due to pumping of deep groundwater and drainage of phreatic groundwater. However, a reduction of groundwater extraction for drinking water may be difficult to establish, in view of the demands of the drinking-water industry. Secondly, measures are needed inside the nature reserve to diminish the undesirable effects of internal eutrophication and acidification caused by a decrease in upward seepage. These may include turf-stripping and trench-cutting (Marrs 1993). Turf-stripping removes the eutrophicated topsoil, and has the additional favourable effect that wetter conditions are created in the remaining topsoil by lowering of the surface level. In order to minimize the adverse effects of the removal of topsoil, which include destruction of vegetation and removal of the seed bank, this should only be practised after careful consideration. Shallow trenches increase the surface runoff of surplus precipitation in winter and in this way prevents downward seepage and acidification processes. Over the short term, adaptations of the drainage system in a buffer zone around nature reserves appear to be very promising. Several measures are possible to decrease the discharge of groundwater in such a buffer zone, for example maintaining higher water levels in ditches and partial or total infilling of ditches.

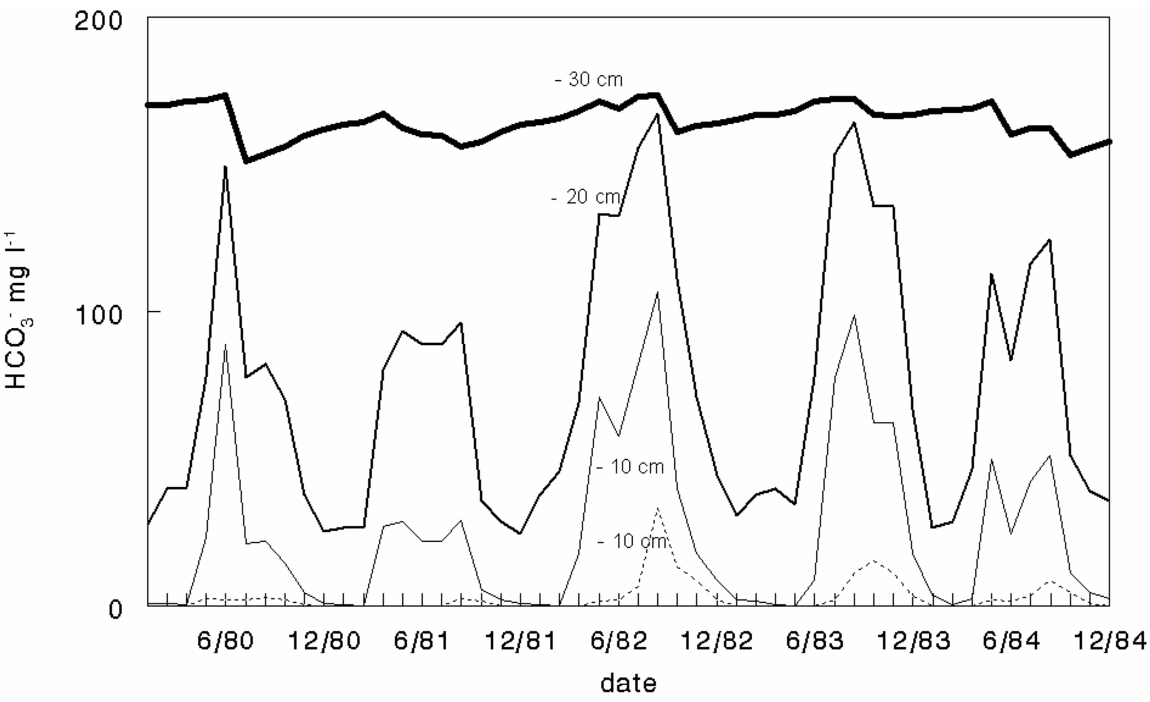

Figure 6. Calculated course of the HCO_3^- concentrations in the soil solution at 10-cm depth without ditch- infilling (- - -) and at various depths in soil with ditch-infilling in the surroundings of the reserve (—). The calculations were carried out with a combination of the hydrological models MICROFEM and ONZAT.

We used hydrological models of the study area to predict the impact of various combinations of the above measures on the extent of upward seapage and rainwater infiltration in the nature reserve. Although integrated, non-steady-state models of groundwater flows applied to the saturated and the unsaturated zone are prefered, in practice simpler models had to be used, due to the limited availability of data. For predicting hydrological impacts of some planned measures in the surroundings of the Bennekomse Meent, we used MICROFEM, a steady-state model for the saturated zone (Hemker & Van Elburg 1988), and ONZAT, a non steady-state model for the unsaturated zone (Van Drecht 1983).

The model calculations predicted that the infilling in of the bordering ditch would result in a 15-cm elevation of the groundwater level at site A in summer. The contribution of calcareous seepage water to the soil water in the root zone was predicted to increase from 0 to 25% at a depth of 10 cm and from 20 to 90% at a depth of 30 cm in summer. The increased upward discharge in combination with the capillary rise would bring HCO_3^- rich water into the root zone and restore the buffer capacity against acidification (Figure 6). This means that the infilling of the 1-m deep ditch would be effective in restoring the characteristic soil chemical conditions in the margins of the reserve.

Other predictions were that the infilling of ditches in the surroundings of the nature reserve would result in the required increase in upward seepage and in higher water levels over the whole reserve. In the surroundings, the higher water levels would be accompanied by an increase in infiltration and acidification. In summary, this study showed that such hydrological models could be very useful in planning drainage systems for nature restoration projects. Based on this prediction the recommended measures were implemented in 1994–95 and a monitoring study has been initiated to follow the effects.

Effects of restoration measures in wet, nutrient-poor fens and fen meadows have already been monitored in several other test projects in The Netherlands. They indicate that the discharge of precipitation by shallow trenches reduces acidification of meadow soils and stimulates upward seepage (Kemmers et al. 1994; Van der Hoek et al. 1994). Particularly at plots where trenching was combined with turf-stripping, the characteristic wet, nutrient-poor site conditions were restored and, within four years, some typical plant species, *Parnassia palustris, Carex panicea*, *Carex oederi and Juncus tenageia*, were re-established. If the exploitation of deep groundwater for drinking water and industrial purposes is not reduced in the near future, it will be necessary to extend such measures gradually to whole nature reserves and repeat them at regular intervals to conserve the last few *Cirsio-Molinietum* communities that were once so common in The Netherlands.

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5

Effectiveness of turf stripping as a measure for restoring species-rich fen meadows in sub-optimal hydrological conditions

Van der Hoek, D. & Heijmans, M.P.D.

turf stripping of acidified fen meadow

Summary

Most species-rich fen meadows in nature reserves in The Netherlands are acidified, due to weaker upwelling of base-rich groundwater. The present study investigated whether and why turf stripping combined with superficial drainage promotes the long-term recovery of such meadows and restores the nutrient-poor, buffered conditions they require. In a field experiment we analysed changes in vegetation composition, soil parameters, groundwater level and groundwater chemistry in stripped plots of degraded *Cirsio-Molinietum* vegetation over twelve years.

After the first five years, many species from the target communities occurred in stripped plots. However, the later succession towards more acidophylous plant communities indicated a weak and decreasing buffer capacity. Though turf stripping exposed a nutrient-poor soil layer with a greater acid-buffering capacity, this success was temporary, because calcium concentration in the groundwater declined during the twelve years. However, the soil pH of the stripped plots increased significantly over time. Since sulphate concentration decreased significantly in the groundwater, whilst the bicarbonate concentration increased, we inferred there was internal alkalinisation driven by sulphate reduction in low-lying stripped plots. In addition, we found that excess precipitation was discharged as surface runoff in the stripped plots during prolonged wet periods.

Internal alkalinisation and the runoff of excess precipitation are the driving processes for some proton neutralisation. However, these positive effects of turf stripping were found to fade away after about twelve years.

Introduction

Since 1990, rewetting and removal of sods (or turf) by stripping have been carried out on a large scale in brook valley meadows in the Netherlands to reverse damage inflicted by drainage, manuring, fertilisation and the acidifying effects of the atmospheric deposition of nitrogen compounds and sulphate. The analysis of successful and unsuccessful projects has shown that such restoration measures have succeeded in nature reserves, but mainly in sites with permanent upward seepage of calcareous groundwater where populations of target species occurred not very long ago (Jansen et al. 2000, 2004). Therefore it was concluded that the only way to restore acidified fen meadows in brook valleys be to their original state was by restoring the regional hydrological system and the concomitant supply of calcium and bicarbonate (so-called external alkalinity).

Implementing hydrological measures in or near nature reserves is often sufficient to restore fen meadow communities that depend on local groundwater systems in shallow aquifers (Jansen et al. 2000). However, the restoration of fen meadows that depend on regional hydrological systems is less likely to succeed, because it is generally not feasible to restore a structural upward groundwater flux by terminating extensive drainage or groundwater abstraction. Despite this, in several Dutch nature reserves and their surroundings, technical measures (such as the infilling of deep ditches) have been applied in the hope of stimulating the upwelling of calcareous groundwater into the root zone (Grootjans et al. 2002). Blocking or infilling of drains in nature reserves may cause an upward seepage flux to be diverted to the surface, but only if local conditions allow such a flow. If this is not the case, the seepage will be diverted to outside the reserve. Whether or not this happens depends on the hydraulic head, geohydrological conditions and size of the reserve (Van der Schaaf 1998).

To combat the acidifying effects of the accumulation of acid precipitation water after drains have been blocked or filled, shallow open drains are often cut to discharge precipitation superficially and prevent the formation of rainwater lenses above the calcareous groundwater (Wind 1986, Poot & Schot 2000). This superficial drainage is also expected to stimulate the upward seepage of calcareous groundwater.

In addition to local hydrological measures, sod stripping has been used successfully to create wet, nutrient-poor soil conditions with a high base saturation, in order to prevent endangered fen meadow species (Grootjans et al. 2002) becoming locally extinct. This led Jansen et al. (2000) to conclude that a combined treatment of sod stripping and superficial drainage may enhance base-rich conditions and thus enable target species to recover in areas where the hydrology has been slightly disturbed. However, Jansen and Roelofs (1996) doubt whether sod removal will result in recovery of *Cirsio-Molinietum* communities in the long run since, in addition to the increase of bicarbonate by sulphate reduction (internal alkalinisation), there might be an increase in the availability of phosphate (called internal eutrophication).

Internal alkalinisation occurs under anoxic, reducing conditions during wet periods in winter and spring. It results from the reduction of iron oxides or sulphate (Ritsema & Groenenberg 1993; Van Haesebroeck et al. 1997; Roelofs 1991; Lucassen 2004; Kemmers et al. 2003). These processes are proton-consuming (Eq. [1] & [2]) and may increase the Ca^{2+} saturation of the cation adsorption complex (CEC) of the soil (Eq. [6]). Moreover, the bicarbonate produced will buffer the protons (Eq. [5]). As a consequence of these processes the soil pH will rise.

In fens with upward groundwater flux, Lucassen (2004) found that the formation of iron sulphides is limited, because sulphate reduction is inhibited in the presence of high concentrations of iron and nitrate, which are better electron acceptors. Internal alkalinisation may take place after sites where upward seepage used to occur have been rewetted. Rewetting by water retention, for example, decreases upward groundwater seepage (Van der Schaaf 1998) and hence reduces the supply of cations and electron acceptors (iron and nitrate) to the topsoil. When iron and nitrate are depleted, sulphate reduction is no longer inhibited. The resulting sulphide production will reduce the iron complexes, which results in the formation of pyrite (FeS_2, Eq. [2+3]). Consequently, periodic drought may lead to oxidation of iron sulphides and to the production of acid (Eq. [4]). Grootjans et al. 2003 found a severe acidification during the summer season in some restoration projects of fen meadows where the soil was rich in pyrite. In addition, pyrite formation involving iron oxides and hydroxides from Fe~P compounds results in the release of phosphate. Such internal eutrophication has been found in fens as a consequence of the supply of sulphate-rich water (Roelofs 1991, Lamers et al. 1998).

Box 1. Key biogeochemical processes for the base status of fen meadows

oxidation of organic matter

$$4\ Fe(OH)_{3(s)} + CH_2O_{(s)} + 7\ H^+ \rightarrow 4\ Fe^{2+} + HCO_3^- + 10\ H_2O \quad [1]$$

$$4\ CH_2O_{(s)} + 2\ SO_4^{2-} + H^+ \rightarrow 2\ HCO_3^- + H_2S + HS^- + 2\ CO_2 + 2\ H_2O \quad [2]$$

pyrite formation and oxidation

$$Fe^{2+} + H_2S \rightarrow FeS_{2(s)} + 2\ H^+ \quad [3]$$

$$4\ FeS_{2(s)} + 15\ O_2 + 14\ H_2O \rightarrow 4\ Fe(OH)_{3(s)} + 16\ H^+ + 8\ SO_4^{2-} \quad [4]$$

proton neutralisation

$$HCO_3^- + H^+ \leftrightarrow H_2O + CO_2 \quad [5]$$

$$2\ Exch\text{-}H^+ + Ca^{2+} \leftrightarrow Exch\text{-}Ca^{2+} + 2\ H^+ \quad [6]$$

Within the scope of hydrological changes an important question is, whether changes in hydrological conditions may cause irreversible changes in soil properties (Faulkner & Richardson, 1989). Following Van Breemen (1987), Kemmers et al. 2003 hypothesised that because redox processes facilitate the exchange of protons for calcium ions, the soil will only be recharged with cations successfully if it has sufficient redox capacity. Dutch sites where restoration had failed had earlier changed from discharge into recharge areas, which might have caused iron depletion by leaching (De Mars 1996) and consequently an insufficient redox capacity for the recovery of the base status of the soil. This hypothesis implies that sod stripping will not permanently restore a high soil base status, because in due course the soil will be leached and acidified again unless the sod stripping is accompanied by a persistent upward flux of groundwater into the root zone.

The question we set out to answer was whether turf stripping (removing the moss carpet and organic horizon) combined with shallow drainage would be effective in the long term for the recovery of species-rich fen meadows and the required high buffer capacity of the soil in a sub-optimal hydrological situation. Such a hydrological situation, characterised by a declining upward seepage of base rich groundwater, is very common in The Netherlands. We hypothesised that in addition to external alkalinity, internal alkalinity is a prerequisite for the recovery of the base status of fen meadows and that the internal alkalinity is favoured by the combined effect of sod stripping and superficial drainage.

Methods

Site description

To investigate the effects of turf stripping and shallow drainage on the recovery of the pH-buffering capacity of soil and on the re-establishment of fen meadow species, we started an experiment in an acidified fen meadow in 1991. The effects of these measures on groundwater, soil and vegetation were monitored for twelve years. In this fen meadow the upward flux of calcareous groundwater had declined. The experimental field is located in the Korenburgerveen nature reserve (310 ha) in the east of the Netherlands (51° 59' N, 6° 40' E). It is in the transition zone between a cut-over bog of 250 ha where regeneration is being attempted, and a small stream. The experimental field is part of a fen meadow (14 ha) with nutrient-poor, species-rich plant communities (C*irsio-Molinietum*), as described by Westhoff & Van Dijk 1952.

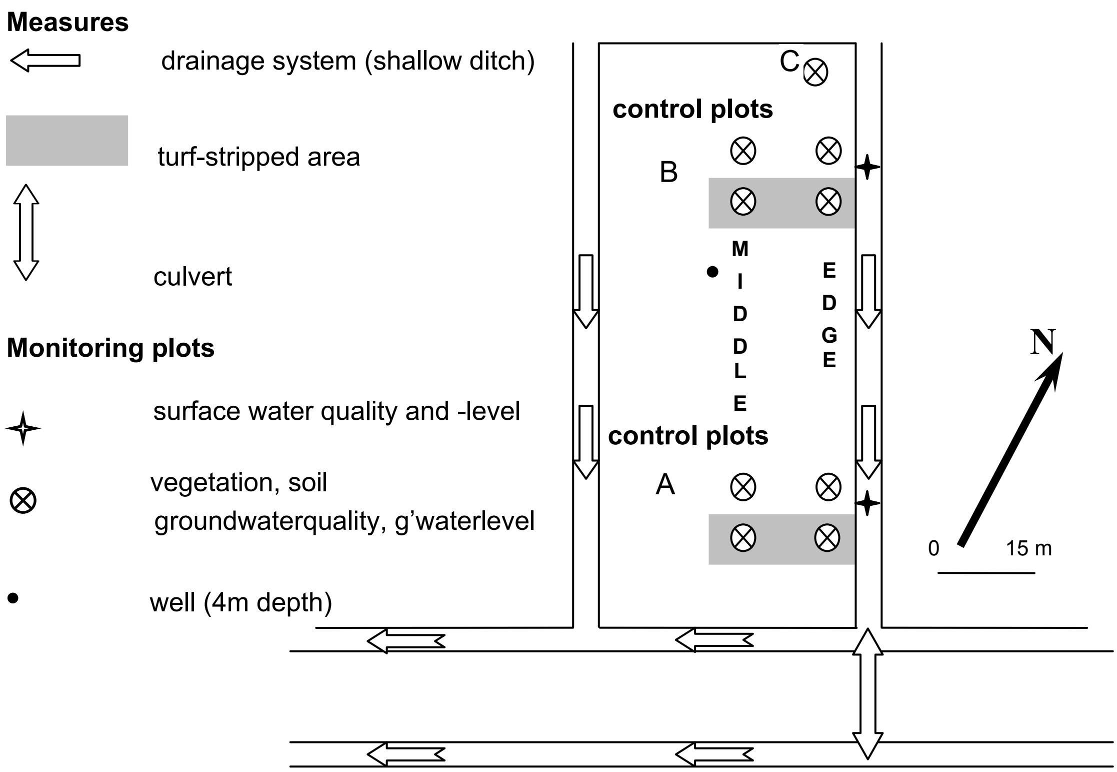


Figure 1: Experimental field with high-lying, low-lying and target plots (sites A, B and C, respectively). Stripped and control plots at edge and middle occur at 2 and 9 m distance from the ditch, respectively, at site A and B. Arrows indicate direction of flow.

During the past twenty years the botanical composition of the fen-meadow has changed gradually. Some rare species, such as *Parnassia palustris*, which indicate calcareous conditions caused by the upward seepage of base-rich groundwater, have decreased in abundance and area. Mosses (*Sphagnum sp.* and later *Polytrichum sp.*) have steadily become more abundant, forming a moss carpet 15 cm thick. The probable main cause of this succession is a steady decline in the upward seepage in the nature reserve. The reserve is surrounded by drained agricultural land and deep groundwater is abstracted for drinking water by a nearby pumping station. However, the occurrence of patches covered with a film of iron oxide from Fe-oxidising bacteria indicates that locally there is still upwelling of groundwater rich in calcium and iron. Further, neither the vegetation composition nor the biomass production indicates any form of internal eutrophication. The biomass production in this fen meadow is probably P- limited, given that the N:P ratio in the total biomass is 38 (Dijkgraaf et al. 1993; Koerselman & Meuleman 1996).

To conserve water in the bog regeneration area, dams have been built and some of the ditches in the surroundings have been filled in. To prevent infiltration of precipitation water, shallow ditches were cut around the experimental field where turf stripping was applied (Figure 1). The water table is regulated with the aim of encouraging the discharge of precipitation excess in wet periods when high groundwater levels occur. The A plots are drained more intensively than the B and C plots, because the soil surface is 5–10 cm higher.

The turf was stripped from two strips (7 x 12 m) bordered by a ditch. It was hoped that removing the vegetation with its moss carpet and underlying organic horizon (O-horizon, 10–15 cm thickness) would encourage the acid rainwater to runoff. By exposing fresh mineral topsoil (OA-horizon) the turf stripping might also create opportunities for the germination of seeds. Seeds of characteristic fen meadow species were present in the low-lying north (site C), and such species do flower in the vicinity. The vegetation at site C was considered to be both a benchmark and a target community for restoration.

Sampling

To monitor the effects of turf stripping on the vegetation, soil and groundwater, we marked out two permanent plots in the middle of each strip and two control plots at distances of 2 and 9 m respectively from the ditch. In addition, we used a permanent plot, in the low-lying northern part of the field (site C), where we expected a relatively strong upward seepage because plant species like *Parnassia palustris* that indicate wet and basic conditions were present. The altitude of soil surface and the wells were measured.

To investigate the initial situation we started sampling in 1991 before the turf stripping. In July of 1991, 1993, 1997, 1999 and 2002 vegetation relevées of all three sites were made according to the Braun-Blanquet nine-step ordinal scale of cover-abundance (Van der Maarel 1979). Nomenclature followed Van der Meijden (1990) for phanerogams, Schaminée et al. (1996) for syntaxa and Margadant & During (1982) for mosses. The top 10 cm of the OA-horizon of the soil was sampled for chemical analysis in every plot in April of 1991, 1993, 1997, 1999 and 2002. The samples consisted of two bulked samples of four sub samples per relevée. They were dried at 35 °C and sieved using a 2 mm mesh.

In each plot we installed two ceramic soil moisture samplers with a porous length of 10 cm and a vacuum syringe to measure the chemical composition of interstitial water and groundwater at depths of 20 and 60 cm below the O horizon. A 4 m deep well in the centre of the field was used to sample deep groundwater. During 1991–2002 the groundwater and the water in the ditches was sampled twice a year, in winter and in summer. The samples were stored at 4 °C in the dark and analysed the next day. In each plot we also installed an observation well at 1 m depth to measure groundwater level. Groundwater level was measured twice a month in all plots. Data from one such well and from the ditch were measured by automatic recorders from April 2001 until September 2002 and used to obtain insight into the short-term groundwater level fluctuations (Rovdan 2003).

Chemical analysis

We measured the following soil parameters: pH-H_2O, pH-KCl, CEC, adsorbed H^+, Ca^{2+}, Mg^{2+}, K^+ and Na^+, organic matter and C content, N-total, P-total, P-water and P-oxalate concentrations. The Fe- and Al-oxalate and pyrite (FeS_2) concentrations were only determined in the soil samples of 2002 (from both the O and OA horizons).

The pH-H_2O and pH-KCl were measured with a combi-electrode in extracts of 20 g soil in 50 ml demi-water or 50 ml 1 M KCl respectively (Houba et al. 1995).

Cation exchange capacity (CEC) was determined after extraction of the soil in a buffered $BaCl_2$ solution at pH = 8.1 (Bascomb, cited by Houba et al. 1995). Samples were equilibrated with a 0.01 M $BaCl_2$ solution after saturation with Ba^{2+} by three extractions with 0.1 M $BaCl_2$. Subsequently, a known excess of 0.02 M $MgSO_4$ was added, causing all Ba^{2+} to precipitate as $BaSO_4$ and occupying all exchange sites with Mg^{2+}. Exchangeable bases (Ca^{2+}, Mg^{2+}, K^+, Na^+) were analysed in the 0.1 M $BaCl_2$ extracts. Ca and Mg were determined by AAS, K and Na were determined by flame emission spectrometry.

Organic matter content was determined by loss on ignition (550 °C, 3 hours).

Total amounts of N and P were measured colorimetrically, after digesting with H_2SO_4 and H_2O_2 in the presence of selenium and salicylic acid (Novozamsky et al. 1983).

The soil samples were extracted with demineralised water to measure P-water and with a solution of ammonium and oxalic acid to measure P-, Fe-, Al-oxalate. A segmented flow analyser used the filtrate for spectrophotometric determination of P-PO_4.

FeS_2 was determined spectrophotometrically after the elimination of Na_3-EDTA soluble sulphates and after extraction with HNO_3.

Titration curves, presenting the relationship between pH and added acid or base, were determined in soil samples of 1999 (both the O and OA horizons) by adding several concentrations of H_2SO_4 and NaOH. The pH was measured in the extract after it had been slowly shaken for two hours and left to rest for 12 hours. The actual acid-neutralising capacity (ANC) was calculated from the inverse slope of the titration curve between the actual pH and the pH that was found after an addition of 0.2 mol H^+ kg^{-1}.

The concentrations of pH, EC, Cl^-, SO_4^{2-}, Ca^{2+}, Mg^{2+}, Na^+, K^+, Fe^{2+}, NH_4^+-N, NO_3^--N, PO_4^{3-} and HCO_3^- in groundwater were measured. The pH and EC_{25} were measured using a combi-electrode. Cl^- was determined by colorimetric titration with silver ions using a Chlor-O-Counter (Temminghoff et al. 2000). SO_4^{2-} was measured spectrophotometrically in a $BaCl_2$-solution. Ca^{2+}, Mg^{2+}, Na^+, K^+, Fe^{2+} were determined by flame atomic absorption spectrometry (AAS). NH_4^+-N, NO_3^--N, PO_4^{3-} and HCO_3^- were analysed colorimetrically, using a continuous flow analyser (SKALAR SAN plus system).

Data analysis

The vegetation data (54 relevées, 88 species) were clustered using TWINSPAN (Hill 1979). Four divisions were used to obtain a limited amount of clusters. Species were grouped into syntaxonomic elements based on their diagnostic value, and the average cover/abundance value of each syntaxonomic element was calculated per cluster. Clusters with similar syntaxonomic composition were merged. The six resulting clusters were summarised into a synoptic table showing presence class and characteristic cover of the species in the different clusters (see Appendix). Species whose frequency is at least 30% higher than in other clusters were considered to be differential.

To investigate the relationship between species composition and environment, mean Ellenberg indicator values of the plant communities were calculated (Ellenberg et al. 1992).

The success of the restoration was evaluated using the number of the Red List species and the characteristic species of the target communities that had re-established.

The effects of turf stripping on soil parameters in relation to the effects of altitude and position (distance to the ditch) were tested for statistical significance using ANOVA, with turf stripping, height and position as factors. The effects of turf stripping on groundwater quality variables were analysed in the same way, including also depth and the season of sampling as factors.

To determine trends over the years we performed a linear regression of each variable against time. The effects of the factors on the regression coefficient were tested using ANOVA.

To ascertain the effect of the measures on groundwater level, data on groundwater levels in stripped and control plots were compared with the water levels in the ditches that border the field (Van der Hoek & Van Walsem 2004). In addition, the effects of shallow ditches and turf stripping on the discharge of atmotrophic water were estimated by simulation with a calibrated SWAP model (Rovdan 2003).

SPSS for Windows (8.0) was used for the statistical calculations.

Results

Plant communities

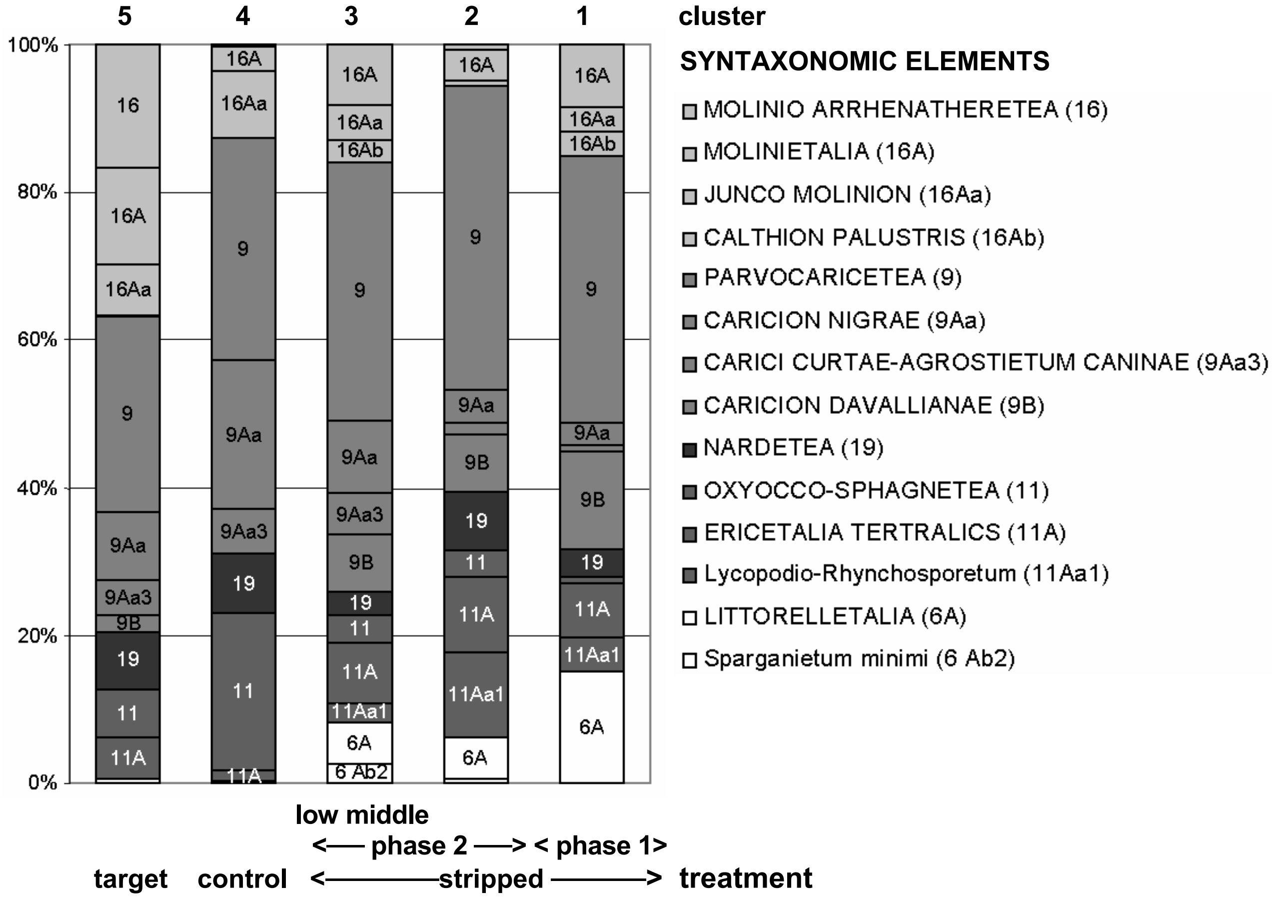


Figure 2. Proportion of syntaxonomic elements in the stripped plots, control plots and the target plot. Stripped plots are differentiated between phase 1 (all plots in the first five years) and phase 2 (all plots in the second five years, including a separate cluster of the low middle plot).

Five clusters were distinguished using TWINSPAN. In addition to the cluster of the target site, the clusters were determined by treatment (phase). The proportion of the dominant syntaxonomic elements is shown in Figure 2 for each plant community. For differential species according to Schaminée et al. (1995, 1996), see the synoptic table (see Appendix).

All the stripped plots have large proportions of *Parvocaricetea* species; elements of *Caricion davallianae*, *Ericetalia tetralicis*, *Lycopodio-Rhynchosporetum* and *Littorelletalia* are also important in the open vegetation. During the first five years after stripping, a plant community of pioneer species (frame community *Juncus bulbosus*-*Carex oederi*, number 1) occurred, which subsequently developed into a mosaic of frame community *Molinia caerulea-Sphagnum palustre* and *Lycopodio-Rhynchosporetum* (plant community 2). The differential species of this cluster are: *Eriophorum angustifolium*, *Dactylorhiza maculata* and *Drosera rotundifolia*.

The vegetation of the low-lying middle plot was dominated by pioneer species during the first three years after stripping. Later on it developed from plant community 1 into a *Carici curtae-Agrostietum caninae typicum* (plant community 3). The positive differential species of this cluster with respect to the species of the other stripped plots are: *Galium uliginosum*, *Lythrum salicaria*, *Juncus conglomeratus*, *Lotus uliginosus*, *Viola palustris*, *Carex curta*, *Parnassia palustris* and *Carex lasiocarpa*. During the succession in the stripped plots the proportion of *Caricion nigrae* species increased at the cost of *Caricion davallianae* species (*Carex oederi ssp. oederi* in particular).

In contrast, the dense vegetation of the control plots (derivate community *Polytrichum commune*, number 4) is characterised by the differential species *Polytrichum commune* and *Carex echinata*.

The vegetation in the low-lying northern part of the field (site C) was classified as a *Carici curtae-Agrostietum caninae,* subass. *Juncetosum acutiflori* (plant community 5, Staatsbosbeheer 2002) as a consequence of the prevailing *Junco-Molinion* elements and the presence of diagnostic species such as *Parnassia palustris*. The plant community at this site corresponds to the original vegetation of the whole study area as described by Westhoff & Van Dijk (1952), except for a higher cover of *Polytrichum cf. commune*, the presence of *Pedicularis palustris* and *Polygala serpyllifolia* and the absence of *Ophioglossum vulgatum*. This succession indicates a slight decrease in soil pH. We considered the vegetation of site C to be the maximum realisable target community and the abiotic conditions at site C to be the target for restoration.

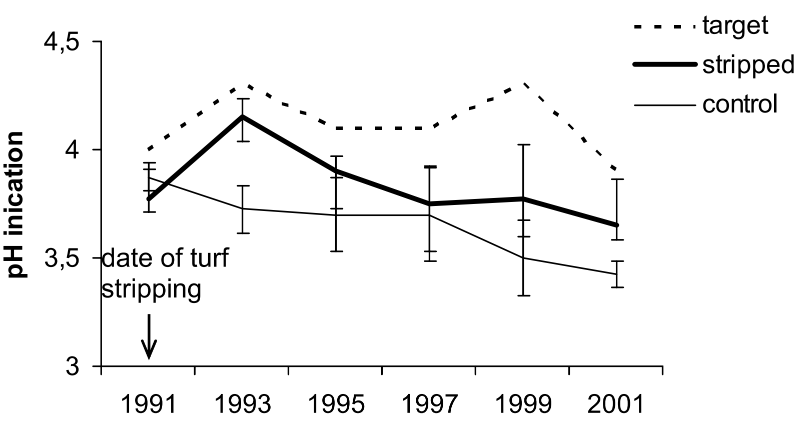


Figure 3. pH indicator value according to Ellenberg of the vegetation in the stripped, control and target plots. Values are means ± SE. The negative trend in the control plots is significant ($P < 0.01$).

The plant communities of the stripped plots indicate that these plots are wetter than the control plots (mean moisture values about 8.5 and 7.9, respectively). In addition, the vegetation indicated a slightly increased availability of nitrogen (not shown) and a higher pH (Figure 3) in the first years after stripping, similar to the values in the target site; subsequently, both values declined. Initially, the buffered conditions were successfully restored, but this was only temporary.

More red list species were found in the plant communities of the stripped plots than in the control plots and their number was constant (table 1), whereas in the control plots they decreased to zero. In the target plot the number of endangered fen meadow species decreased from 10 to 4 within the twelve years.

Table 1. Occurrence of endangered fen meadow species (red list species) in the stripped, control and target plots. *) : before stripping.

	target						**control**						**stripped**					
	91	93	95	97	99	01	91	93	95	97	99	01	91*)	93	95	97	99	01
Red list species																		
Carex lasiocarpa		x	x										x		x	x		x
Dactylorhiza maculata	x	x	x	x	x		x		x	x	x					x	x	
Dactylorhiza majalis															x			
Drosera intermedia														x	x	x	x	x
Drosera rotundifolia			x															
Menyanthes trifoliata	x	x	x	x	x					x			x	x			x	x
Parnassia palustris	x	x	x	x	x										x			
Pedicularis palustris	x	x					x						x					x
Pedicularis sylvatica		x	x	x				x	x					x		x	x	x
Polygala serpyllifolia	x	x	x										x					
Potentilla palustris		x	x	x	x	x								x	x	x		x
Rhinanthus minor	x	x	x	x	x	x												
Succisa pratensis					x	x				x	x							
Valeriana dioica			x	x	x	x												
Viola canina		x																
# Red list species	6	10	10	7	7	4	2	1	2	3	2	0	4	4	5	5	4	6

Soil

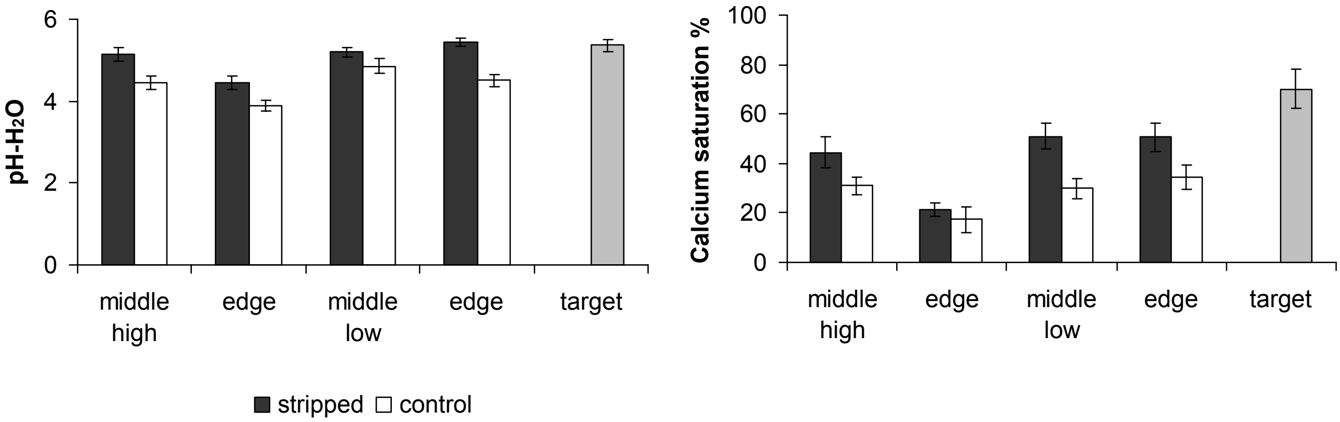
The overall effect of turf stripping on pH-H_2O and on the variables indicative for the buffering capacity was positive (table 2, Figure 4). In addition, topographical height and position did have significant effects, which generally resulted in higher pH values in low-lying plots (B) and lowest values in the edges of the high-lying plots (A).

The absence of an overall effect of turf stripping on the organic matter content and CEC of the sampled OA horizon is probably due to only the organic topsoil being removed. The N-total ranged from 2.8 to 5.6 g kg^{-1} and had hardly decreased as a result of stripping.

Table 2. Effects of turf stripping, height and position on soil variables. F- values with their levels of significance (^{x} $p < 0.05$, ^{xx} $p < 0.01$, ^{xxx} $p < 0.001$, ANOVA with stripping, height and position as factors). No significant effects on CEC, P-water and P-total were found.

Factor Variable	Turf stripping (S)	Height (H)	Position (P)	S x P	S x H x P	H x P
pH-H_2O	38.3^{XXX}	25.4^{XXX}	10.9^{XX}			7.6^{XX}
pH-KCl	84.9^{XXX}	60.2^{XXX}	27.7^{XXX}		7.7^{XX}	19.9^{XXX}
Base-sat	17.6^{XXX}	21.9^{XXX}	6.1^{X}			9.2^{XX}
Ca-sat	15.6^{XXX}	16.1^{XXX}	7.3^{XX}			11.1^{XX}
% org matter				7.0^{X}		
N-total	4.5^{X}			7.3^{XX}		
P-oxalate	9.8^{XX}		7.5^{XX}			

The P-total and P-water concentration in the top 10 cm were influenced neither by stripping, nor by height and position. However, P-oxalate was significantly lower in the stripped plots, with the smallest values occurring in the edges of these plots (Figure 4). P-water did not differ between the plots and decreased significantly from 41.0 mg 100 g^{-1} in the first years to 5.4 mg 100 g^{-1} at the end of the twelve years.



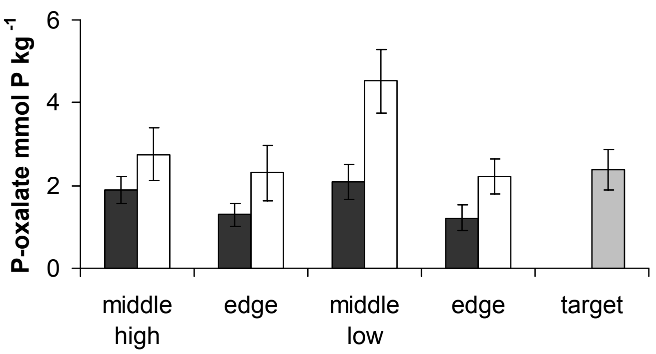


Figure 4. pH-H_2O, calcium saturation of the CEC and P-oxalate concentration in soil of the stripped and control plots as a function of height and position. Bars are means ± SE of both seasons. The value in the target plot is shown as a benchmark.

Apart from P-water, the only significant trends in time were found in pH-H_2O and pH-KCl. Both these pH values increased in time, but only in the stripped plots (Figure 5). A positive effect of stripping on the ANC of soil (OA horizon) was found (ANOVA $p < 0.05$) in 2002 (table 4). Iron appeared to be present as pyrite and iron oxides but we found no significant overall effects of stripping, horizon, height and position. On pyrite of stripped plots, a significant interaction between stripping and horizon ($p < 0.05$) was found; it is attributable to the high pyrite content of the O-horizon of the control plots.

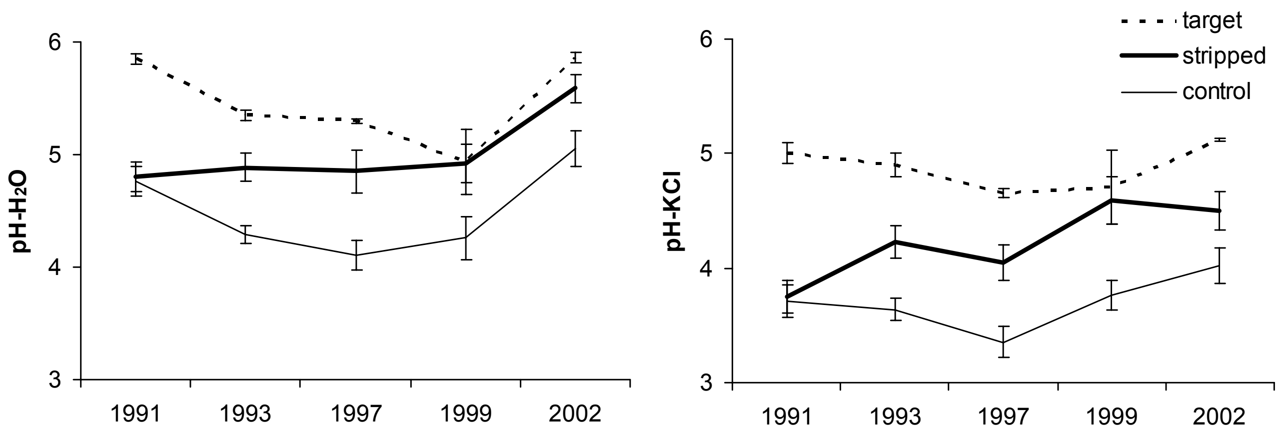


Figure 5. pH-H_2O and pH-KCl of soil in stripped, control and target plots. Trends in stripped plots are significant (pH-H_2O: P = 0. 003 and pH-KCl: P = 0. 002).

Groundwater

The bicarbonate and calcium concentrations in the groundwater were influenced by turf stripping, and depended on height and position (table 3). In the stripped plots, the highest values occur in the middle of the low-lying plots (B) and the lowest on the edges of the high-lying plots (A) (Figure 6). In addition, bicarbonate concentration is influenced by depth and season, which means that in the stripped plots, relatively high concentrations were found at 20 cm depth in summer. The pH values were in agreement with the concentrations of calcium and bicarbonate. The highest values (6.42 ± 0.05) were measured in the centre of low-lying plots, whereas the lowest values (5.87 ± 0.07) occurred in the edges, especially the edges of the highest plots. However, no significant effect of stripping was found on the pH of the groundwater. The mean sulphate concentrations were low (max. 20 mg l^{-1}), especially in stripped plots, and they decreased with depth. Ammonium and nitrate concentrations were less than 0.5 mg l^{-1} and also decreased with depth, but were not significantly influenced by stripping (table 3).

The only significant trends identified in the twelve years were in the calcium, bicarbonate and sulphate concentrations. In the summer, the decrease of the calcium concentration at 60 cm depth was significantly greater in the low-lying plots (Figure 7). The biggest decrease occurred in the target site C and in deeper groundwater, from about 137 mg l^{-1} in the beginning to 57 mg l^{-1} at the end of the monitoring. Consequently, after the twelve years, the calcium concentration at 60 cm depth in summer had the same low value in all sites. By contrast, the bicarbonate concentration increased significantly, especially in the stripped low-lying plots (Figure 7). Bicarbonate concentration also increased in the target site, from about 250 to 350 mg l^{-1}, but not in the deep well, where concentrations fluctuated around 400 mg l^{-1}.

Table 3. Effects of turf stripping, height, position, depth and season on groundwater quality. *F*- values with their levels of significance (^{x} $p < 0.05$, ^{xx} $p < 0.01$, ^{xxx} $p < 0.001$, ANOVA with stripping, height, position, depth and season as factors). No significant effects on P-concentration were found.

Factor	**Turf stripping**	**Height**	**Position**	**Depth**	**Season**	**H x P**	**S x D x Se**
Variable	**(S)**	**(H)**	**(P)**	**(D)**	**(Se)**		
Ca^{2+}	4.1 ^{X}	40.9 ^{XXX}	35.4 ^{XXX}				
HCO_3^-	19.7 ^{XXX}	43.5 ^{XXX}	25.8 ^{XXX}	23.2 ^{XXX}	14.9 ^{XXX}		
SO_4^{2-}	8.6 ^{XX}			10.8 ^{XX}			
pH		23.3 ^{XXX}	28.5 ^{XXX}			7.5 ^{XX}	4.4 ^{X}
NH_4^+				7.0 ^{XX}			
NO_3^-				5.3 ^{X}			

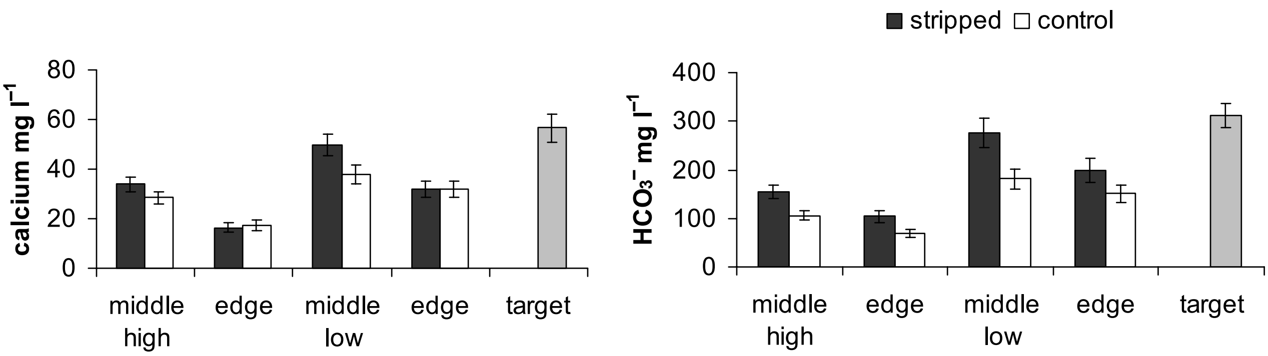


Figure 6. Calcium and bicarbonate concentration in groundwater (20 and 60 cm depth) from stripped and control plots as a function of height and position. Bars are means ± SE of both seasons. The value of the target plot is shown as a benchmark.

Figure 8 shows a significant overall decrease of sulphate concentration at 20 and 60 cm depth over time. The strongest trend was found in the stripped plots (Figure 8). The sulphate concentrations in the target site were always relatively low. A marked trend was found in the deep groundwater over the twelve years: the sulphate concentration increased significantly from about 10 mg l^{-1} to 30 mg l^{-1}, which might indicate an increasing supply of local shallow groundwater.

Figure 9 shows that ditches drain the experimental field nearly the whole year, which suggests that there is still some upward seepage. Only in dry periods does surface water infiltrate from the ditch into the field, due to the relatively deep groundwater levels. During prolonged wet periods, groundwater levels were at the surface; with the consequence that excess precipitation was discharged as surface runoff, especially in the stripped plots.

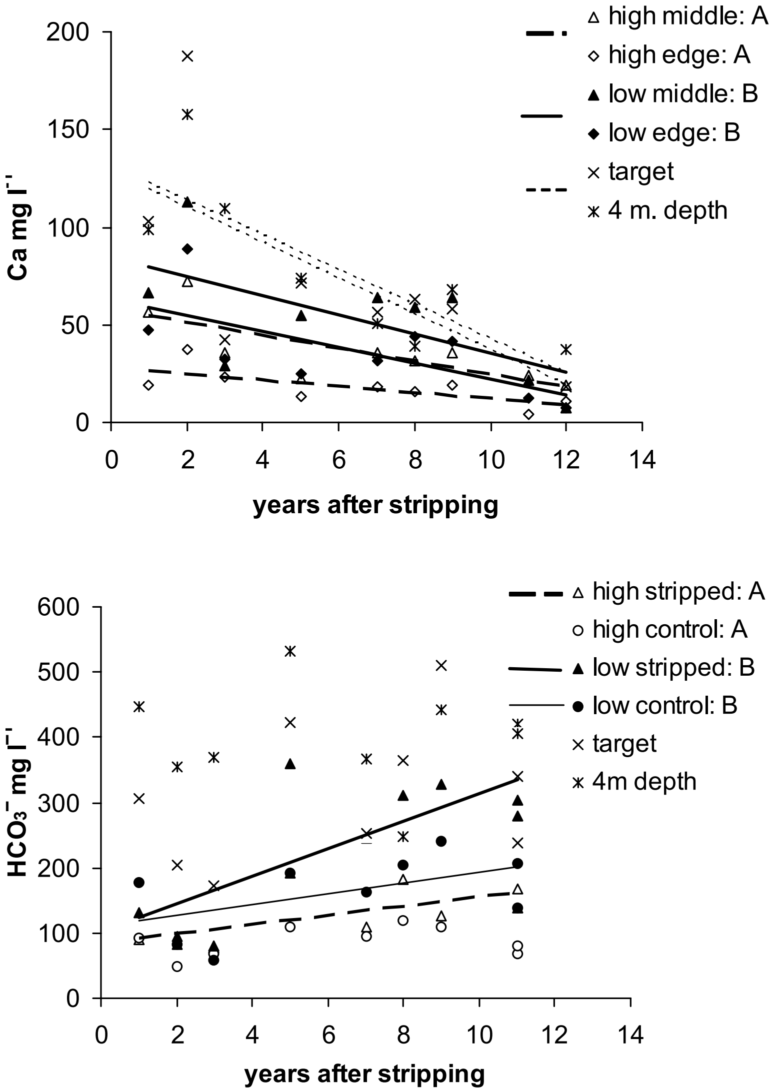


Figure 7. Mean calcium and bicarbonate concentrations in groundwater (at 60 cm and at 20 & 60 cm depth, respectively) from stripped and control plots in years after stripping as a function of height (A = high, B = low) and position. For calcium values and significant trends combined from stripped and control plots are shown, while they are shown separately for bicarbonate. Significance levels of lineair trends for calcium: low middle and edge $P < 0.005$, high middle and edge $P < 0.001$; for bicarbonate: high stripped $P < 0.005$, low stripped $P < 0.001$, low control $P < 0.005$. Values and trends in the target plot and at 4 m depth are shown as a benchmark.

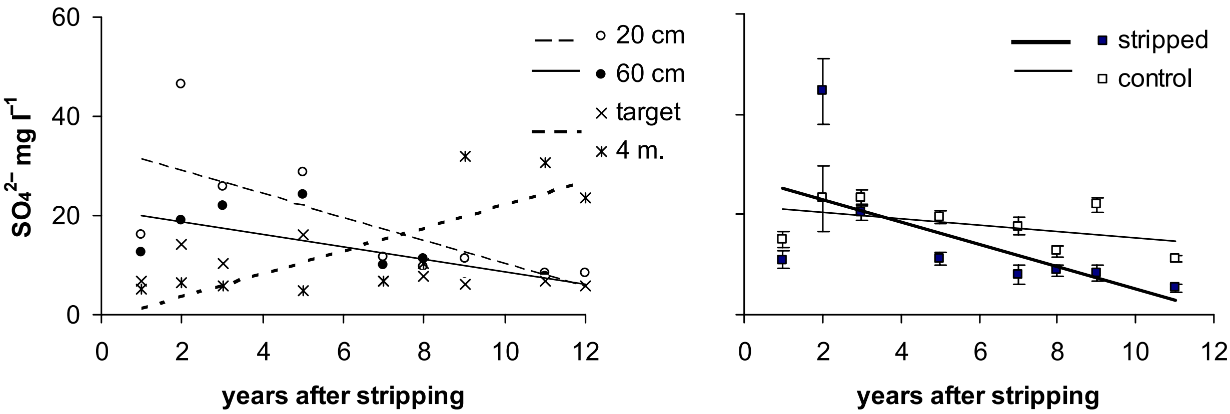


Figure 8. Sulphate concentration in groundwater in years after stripping. All trends shown are significant ($P < 0.001$). At left, mean values at 20 and 60 cm combined from stripped and control plots are shown. Mean values of the target plot and at 4 m depth are shown as a benchmark. At right, mean values in groundwater at 20 cm depth from stripped and control plots (in winter) are shown separately.

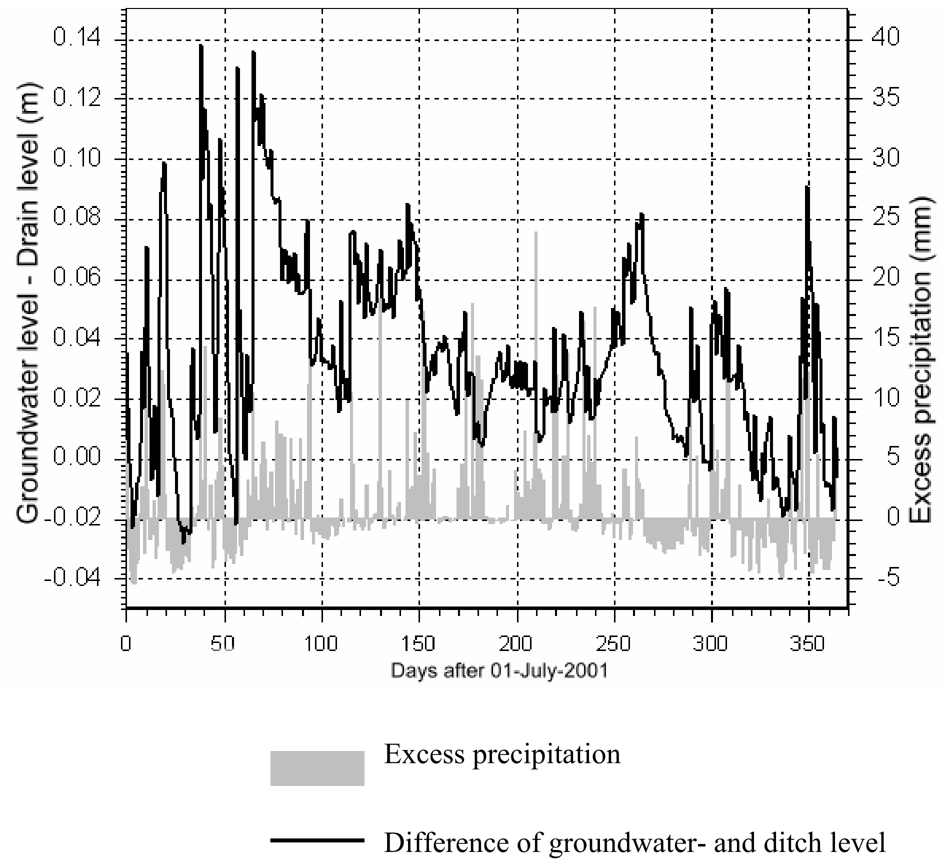


Figure 9. Excess Precipitation (in bars) and differences of groundwater and drain level during one year. Positive values mean groundwater level is higher. Water levels and precipitation have been calculated from high frequency measurements (4x h^{-1} and 1x day^{-1}, respectively). Groundwater levels were monitored at 15 m distance from the ditch (figure provided by S. Van der Schaaf).

Discussion

The questions in our study were whether and why turf stripping, combined with shallow drainage, is effective for the long-term recovery of species-rich fen meadows and the required high buffer capacity of the soil. We expected that not only external alkalinisation but also internal alkalinisation would be an important process in the recovery of acidified fen meadows within a nature reserve with sub-optimal hydrological conditions.

As our results show, the combination of turf stripping and superficial drainage can stimulate the re-establishment of fen meadow species for many years. Even some red list species re-established. However, we agree with Jansen et al. (2000) that complete recovery of plant communities similar to those present in the past is impossible. There are two reasons for this. Firstly, restoration is hampered by the impossibility of the re-establishment of locally extinct plant species, such as *Ophioglossum vulgatum* and *Cirsium dissectum*. These species appeared to be absent from the soil seed bank (Westhoff & Van Dijk 1952) and neither do they occur in the vicinity from where they could have dispersed (Podschlod et al. 1996; Bakker & Berendse 1999). Secondly, the high base saturation of the soil, which is a prerequisite for successful restoration, was recovered only temporarily. Given these circumstances and the high groundwater levels all over the year (Bell Hullenaar 2004), the best result from stripping one can expect is for some of the disappeared species to re-establish and the vegetation to approach the composition of the nearby local reference vegetation, which is according Jansen et al. 2004.

The recovery of buffered conditions succeeded best on the low-lying stripped plots, owing to the presence of calcareous groundwater and the effectiveness of superficial drainage (Van der Hoek & Van Walsem 2004). However, the presence of some target species characteristic of the *Junco-Molinion*, e.g. *Parnassia palustris*, at those plots was only transient. The vegetation of the stripped plots changed into a *Caricion nigrae* plant community at the expense of species of the *Caricion davallianae*, which indicates a gradual acidification. This acidification might have been caused by a decrease in the upward seepage of calcareous groundwater (external alkalinity), since the calcium concentration of groundwater decreased over time at all depths.

The investigation of the chemical composition of groundwater and soil confirmed our hypothesis that apart from external alkalinisation, internal alkalinisation might play a role in the recovery of the acid buffering capacity of fen meadows, especially in stripped plots. Firstly, we found increasing bicarbonate concentrations together with decreasing sulphate concentrations in shallow groundwater, which might have been caused by sulphate reduction. The concentrations of iron oxides and pyrite measured in stripped and control plots (OA horizon, Table 4) indicate that the conditions are still favourable for the reduction of iron and sulphate and the consequent proton consumption and bicarbonate production (Kemmers et al. 2003). Secondly, we found a reduced infiltration of precipitation water in the stripped plots. Evidence for the reduced infiltration, a consequence of a stimulated run off, was the higher EC and calcium and bicarbonate concentrations of groundwater in the middle of the experimental field (Van der Hoek & Van Walsem 2004) and was calculated by Rovdan (2003). Rovdan (2003) described the dynamics of groundwater level in the experimental field using the calibrated SWAP model (Kroes & Van Dam 2003) and confirmed our finding that the ditches continued to drain even in wet periods. In addition, Rovdan's simulation with SWAP demonstrated the positive effect of stripping on the discharge of precipitation excess and on the fraction of groundwater transported from the mineral subsoil to the soil surface. Both mechanisms, internal alkalinisation and precipitation runoff, resulted in an increasing pH and a mean calcium saturation of CEC up to 50-60 %, in the soil of the stripped plots. Similar increased pH values, combined with a rise in endangered species, were found in wet heaths after sod cutting and lime application (Dorland 2004).

The vegetation succession in our fen meadow, however, indicated an ongoing acidification, which suggests that the buffer capacity had not sufficiently recovered in the stripped plots for the long-term. We always found a lower buffer capacity in stripped plots than in the target plot, in addition. The indicated acidification might be the result of increased mineralisation and oxidation of sulphides (e.g. pyrite) in dry periods, although the pH values in the soil did not show the periodically low values that were reported by Grootjans et al. (2003) and described by Kemmers (2003).

We conclude that the presence of a sufficient redox capacity might have facilitated the recharge of the cation adsorption complex with calcium ions in wet periods, which supported the cation-exchange buffering mechanism in the beginning. Although the cation adsorption complex could have been recharged in the beginning after turf stripping, especially in the low-lying plots, we expect that overall acidification will continue, since there was a significant overall negative trend of the calcium concentration in groundwater and protons will only be buffered weakly by the bicarbonate produced by sulphate reduction. Based on the titration curves determined in laboratory, which show a sharp rise in pH after the addition of bases, we conclude that the acidification of our fen meadow soils can quickly be reversed after stripping, if the upward seepage of base rich groundwater increases in the short term.

The low ANC in the control plots (Table 4) shows that the buffer capacity was not restored. On the contrary, the drainage that would have occurred without stripping of these plots might have resulted in an increased infiltration of precipitation water and leaching of calcium, as was found by Heathwaite (1991) in a fen and by Kemmers et al. (2001) in a fen meadow. More severe effects of leaching on buffer capacity have been found in the O-horizon of the control plots where the ANC was lowest (table 4), in spite of the presence of sufficient redox capacity and pyrite (Kemmers & Van Delft 2003). It seems that reduction processes are barely able to generate effective internal alkalinisation for acid buffering when there is insufficient calcium. Without stripping, the fen meadow may develop towards a bog vegetation, as a consequence of the increased contribution of precipitation water at the expense of groundwater (Wheeler & Shaw 1995) and because *Sphagnum sp*. contributes to the acidification by active cation exchange (Verhoeven & Liefveld, 1997).

Table 4. Acid neutralisation capacity (ANC, after addition of 0.2 mol H^+ kg^{-1}), pyrite (FeS_2) and iron-oxides (Fe-oxalate) of the O and OA horizon of the soil of stripped and control plots in 2002. Values are means ± SE. Values sharing a letter are not significantly different (at α = 0.05 Tukey's post-hoc test).

	O-horizon		**OA-horizon**	
	stripped	**control**	**stripped**	**control**
ANC $mol_c\ kg^{-1}$ $mmol\ l^{-1}$		0.9± 0.1 ^{b}	5.6± 2.7 ^{a}	1.7± 1.0 ^{ab}
pyrite mg (FeS_2) 100 g^{-1}	443.7± 16.5 ^{p}	809.4± 160.9 ^{q}	516.6± 97.6 ^{pq}	456.5± 66.7 ^{p}
Fe-oxalate mg 100 g^{-1}	340.9± 23.5 ^{xy}	399.3± 58.7 ^{y}	225.3± 45.2 ^{x}	251.3± 64.5 ^{x}

In general, the availability of N and P in the soil is low, and stripping caused an even larger decrease in P-oxalate in the soil. Moreover, the value of P-water in the soil decreased with time. From this we conclude that nutrient-poor conditions persist. Phosphate mobilisation by internal eutrophication (Lamers et al. 1998) did not occur in our mesotrophic fen meadow ecosystem, since iron had not been depleted, sulphate concentrations were low and consequently sulphate reduction was weaker compared to fens (Lucassen 2004). We infer that plant growth in our fen meadow might have been more limited by factors other than N and P availability, such as water chemistry features (pH). Verhoeven et al. (1990) made the same suggestion on plant growth in bogs.

From this study we conclude that turf stripping results in the long-term recovery of nutrient-poor, wet conditions by decreasing the pools and availability of nutrients and by lowering the soil surface. It also results in a soil with a pH buffered in the neutral region for some years, due to the stimulated run off of precipitation water. It can therefore be concluded that in the sub-optimal hydrological conditions prevailing in most fen meadows, turf stripping and some drainage may succeed in restricting ongoing acidification, as these measures stimulate internal alkalinity for a considerable number of years. As a result, endangered fen meadow species characteristic of the local best-buffered conditions, may re-establish. They will probably persist until the upward seepage of base-rich groundwater is ultimately restored by large-scale hydrological measures in the surroundings.

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APPENDIX

Synoptic table of the communities distinguished.

Percentage presence is given, as well as mean cover (superscript). The percentage presence is expressed in six classes: + = 0-5%; I = 6-20%; II = 21- 40%; III = 41-60%; IV = 61-80%; V= 81-100%. The mean cover was calculated from the ordinal values

Plant communities:

1. *FC Juncus bulbosus- Carex oederi [Parvocaricetea]*

2. *Mosaic of FC Molinia caerulea-Sphagnum palustre [Parvocaricetea / Junco-Molinion] and Lycopodio-Rhynchosporetum*

3. *Carici curtae-Agrostietum caninae,* subass. *typicum*

4. *DC Polytrichum commune [Parvocaricetea]*

5. *Carici curtae-Agrostietum caninae,* subass. *Juncetosum acutiflori*

FC: Frame community; DC: Derivate community

Species differentiating between the different clusters of the control and stripped plots are indicated with a grey background. Negatively differentiating species are boxed (criterion for differentiating: 30%).

Plant community (cluster)	**5**	**4**	**3**	**2**	**1**
treatment	**target**	**control**	**stripped**	**stripped**	**stripped**
			low middle	**phase 2**	**phase 1**
Number of relevées	6	28	3	7	9
Mean number of species	33.3	14.0	25.0	21.3	20.0
Standard deviation	4.3	2.5	1.6	2.4	4.3
MOLINIO-ARRHENATHERETEA					
Holcus lanatus	IV ^{2}	+ ^{2}			
Prunella vulgaris	V ^{3}				
Rhytidiadelphus squarrosus	IV ^{4}			I ^{3}	
Ranunculus repens	I ^{3}				
Ranunculus acris	V ^{2}				
Plantago lanceolata	V ^{3}				
Rumex acetosa	V ^{2}				
MOLINIETALIA					
Cirsium palustre	V ^{2}			III ^{1}	II ^{1}
Equisetum palustre	V ^{3}	III ^{2}	V ^{3}	III ^{1}	IV ^{2}
Luzula multiflora	II ^{2}	I ^{2}			
Galium uliginosum	III ^{4}		II ^{3}		
Climacium dendroides	IV ^{3}			I ^{2}	
Lythrum salicaria	V ^{2}	+ ^{1}	V ^{2}	III ^{2}	IV ^{2}

APPENDIX continued

Plant community (cluster)	**5**	**4**	**3**	**2**	**1**
treatment	**target**	**control**	**stripped**	**stripped**	**stripped**
			low middle	**phase 2**	**phase 1**
JUNCO-MOLINION					
Succisa pratensis	II 5	I 2			
Juncus conglomeratus		III 2	V 2		
Valeriana dioica	IV 4				
Juncus acutiflorus	V 2	IV 4	IV 2		IV 2
Differentiating with respect to **CALTHION**:					
Molinia caerulea	V 3	V 5	V 3	III 3	II 2
CALTHION PALUSTRIS					
Carex disticha					I 2
Lychnis flos-cuculi					
Dactylorhiza majalis					I 1
Lotus uliginosus	I 1		V 2	II 1	III 2
PARVOCARICETEA					
Hydrocotyle vulgaris	V 4	II 3	V 3	V 4	V4
Ranunculus flammula		+ 1	IV 2	V 2	V 2
Juncus articulatus	II 3	II 3	V 4	V 3	III 2
Pedicularis palustris	II 2	I 2			
Calliergonella cuspidata				II 3	
Potentilla palustris	V 3		II 1	I 1	II 1
Agrostis canina	V 3	IV 3	V 5	V 5	V 3
Carex nigra	V 6	V 4	V 3	III 3	II 3
Epilobium palustre					IV 2
Eriophorum angustifolium			II 3	V 3	II 2
Galium palustre	III 3		II 2	I 1	IV 2
Sphagnum sp.	V 5	V 5	V 5	V 5	II 1
CARICION NIGRAE					
Viola palustris	IV 4	I 2	V 4	III 1	II 3
Differentiating with respect to **C. DAVAL.**:					
Aulacomnium palustre	IV 4	II 3	II 3	I 3	
Polytrichum cf. commune	V 4	V 8	IV 2	III 3	II 1
C. CURTAE-AGROSTIETUM CANINAE					
Carex curta		I 2	IV 3	I 2	
Carex echinata	V 2	IV 3	II 3	I 2	
Menyanthes trifoliata	V 2	I 2	II 3		I 2
Carex rostrata				I 2	I 2

APPENDIX continued

Plant community (cluster)	5	4	3	2	1
treatment	**target**	**control**	**stripped**	**stripped**	**stripped**
			low middle	**phase 2**	**phase 1**
CARICION DAVALLIANAE					
Parnassia palustris	V 3		II 2		
Carex oederi oederi			V 4	V 4	V 5
NARDETEA					
Potentilla erecta	V 3	V 3	IV 3	V 2	V 2
NARDETALIA					
Viola canina	I 2				
Gentiano pneumonanthes-nardetum					
Pedicularis sylvatica	III 2	I 3	II 1	III 2	I 1
Polygala serpyllifolia	III 2	I 1			
Differentiating with respect to **CALTHION**:					
Dactylorhiza maculata	V 2	II 1		III 2	
OXYCOCCO-SPHAGNETEA					
weak characteristic species					
Erica tetralix		II 2			I 1
Aulacomnium palustre	IV 4	II 3	II 3	I 3	
Drosera rotundifolia	I 1				
ERICETALIA TETRALICS					
Carex panicea	V 5	II 3	V 5	V 6	V 3
Lycopodio-Rhynchosporetum					
Drosera intermedia			II 3	V 5	III 3
Lycopodium inundatum			II 2	III 2	
LITTORELLETEA					
LITTORELLETALIA					
Eleocharis multicaulis				I 2	II 2
Juncus bulbosus			V 4	V 3	V 6
Sparganietum minimi					
Carex lasiocarpa	II 1	+ 2	IV 3	I 2	

6

Effectiveness of rewetting in regeneration of fen meadows

The impact of rewetting measures on key processes in the topsoil of 'De Veenkampen' fen meadow restoration project

Van der Hoek, D. & Kemmers, R.H. 1998. *Landschap* (4): 211-224.

Rewetting by subsurface irrigation with deep groundwater

Summary

In 1986 an experiment to examine the impact of rewetting on nature restoration was started at 'De Veenkampen'. It was intended to achieve the regeneration of wet, nutrient-poor soil conditions by conserving rainwater and by subsurface irrigation. The soils consist of peat with a thin clayey top layer and have been severely affected by forty years of hydrological management and fertilising to support farming practice. Fertilisation has, in particular, resulted in a major accumulation of inorganic P. Soil changes seemed to be irreversible and as a consequence restoration measures might be partly effective. The discussion of the results focuses on the suitability of these sites for the restoration of the *Cirsio-Molinietum*, whose biomass production is P-limited. It seems that the desired nutrient-poor conditions in De Veenkampen will only develop if wet conditions are restored by upward seepage of groundwater.

It appeared that subsurface irrigation with deep groundwater produced higher groundwater levels throughout the year, but this measure was accompanied by acidification of the topsoil. The consequence was a decrease in the mineralisation of nitrogen and an increase in the amount of organic matter. A striking effect was the decrease of plant-available phosphate during the ten years of this experiment. However, contrary to expectations, the current low calcium content of the groundwater does not seriously affect P fixation. The decrease is the result of the dissolution of iron phosphate complexes under the anaerobic conditions and the subsequent leaching of P to the subsoil. The slow decrease in the inorganic P suggests that the nutrient-poor conditions will ultimately be restored.

The calcium-rich site conditions characteristic of a *Cirsio-Molinietum* and favourable for the precipitation of Ca-P salts will be regenerated only if the root zone is penetrated by groundwater containing sufficient amounts of calcium or by alkaline surface water. Conservation of precipitation appeared to be an inadequate measure to restore the high groundwater levels and the nutrient-poor conditions in the topsoil.

Introduction

When restoring species-rich vegetations of wet grassland on peaty soils with a clayey topsoil it is necessary to take account of the irreversible changes in the soil that are the legacy of previous farming practices. It is essential to build up a new nutrient-poor topsoil. Only if rewetting is accompanied by high groundwater levels throughout the year will the pedological changes occur that sufficiently accelerate the desired impoverishment – particularly a sharp fall in the amount of available phosphate. The only way to prevent the soil acidification that frequently accompanies rewetting is for the inflowing water to be strongly buffered.

In the soil of carr peat areas in the Netherlands the availability of nitrogen and phosphorus for plant growth has risen sharply under the influence of the intensification of agriculture. This eutrophication and the lowering of the groundwater level have led to an increase in biomass production and a decline in the species richness of the grasslands.

In accordance with the 1990 Nature Policy Plan of the Netherlands, measures to regenerate species-rich, wet, nutrient-poor grassland are being implemented in an appreciable area of former farmland in the carr peat area. However, the efficacy of the various rewetting and management measures being considered is not adequately known.

Research is being done in De Veenkampen trial area on the repercussions of certain rewetting measures on the recovery of basic, nutrient-poor conditions in the soil. De Veenkampen lies in the south of the Gelderland Valley (Figure 1) and, together with the Bennekomse Meent nature reserve, is in the transition area between the alluvial clay landscape of the Neder Rhine (near Wageningen) and the peat landscape that occurs in the middle of the Valley, between Veenendaal and Ede. The Gelderse Valley is flanked on both sides by ice-pushed ridges: the Utrecht Ridge and the Veluwe. The Bennekomse Meent is a remnant of the extensive, nutrient-poor, species-rich meadows with local occurrences of the orchid-rich meadow vegetation (*Cirsio-Molinietum*) that was present in the southern part of the Gelderland Valley until c. 1950.

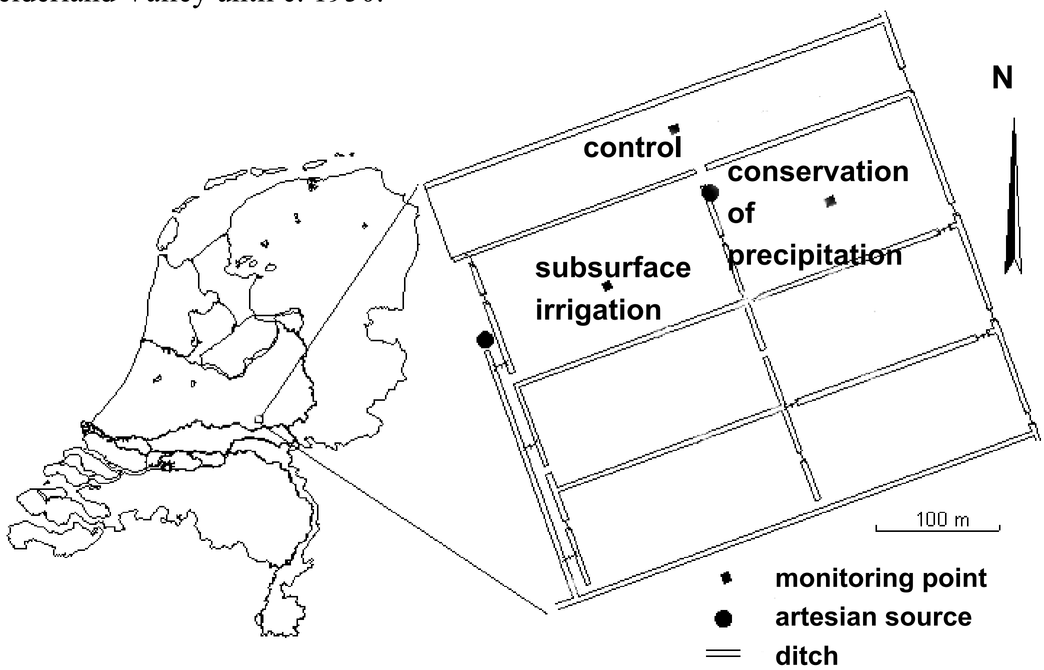

Figure 1. Location of 'De Veenkampen' experimental area and subdivision into compartments with subsurface irrigation, conservation of precipitation and no hydrological measures (control).

This paper presents the results of the monitoring study on the efficacy of rewetting for the restoration of the abiotic conditions in De Veenkampen. The most important research question was: to what extent and how do high groundwater levels and the quality of the groundwater influence the chemical processes in the soil that determine the availability of N and P? It was expected that important control variables such as aeration and pH would change under the influence of the rewetting, causing the availability of nitrogen and phosphate in the soil to decline (Figure 2).

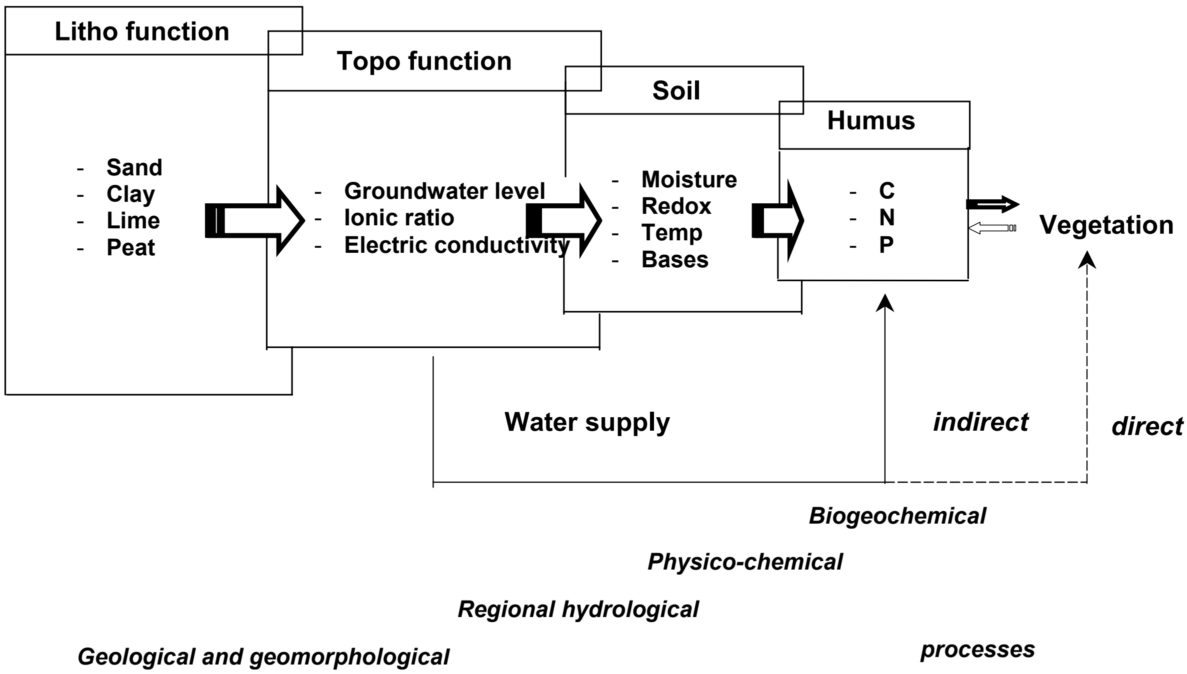

Figure 2. Hierarchical system of processes in different ecosystem compartments controlling site conditions and nutrient recycling (acc. to Kemmers et al. 1995).

First, the experimental set-up and the reference scenario are explained. Then, drawing on the results of the monitoring study, the following issues are discussed: the trends in the level and quality of the groundwater, and the availability of the most important nutrients in the soil during 10 years of rewetting. To conclude, attention is paid to the most important processes that regulate the availability of phosphate in the soil.

Experimental set-up and research method

'De Veenkampen' experimental complex is the site of research on the feasibility of regenerating the vanished wet, nutrient-poor fen meadows on grasslands that used to be intensively managed. The experimental area is 13 ha. As a result of the improved drainage, since 1940 the lower groundwater levels have allowed significant oxidation to take place in the peaty soils of De Veenkampen, which has brought about an increase in the clay content. The soil, once peaty with a clayey topsoil, is now a strong humic clay layer c. 50 cm thick, overlying peat. In addition, and partly as a result of groundwater abstraction in the Veluwe, the upward seepage has been weakened. Most of the weak seepage is nowadays removed via ditches and no longer reaches the root zone. Since 1978 there has been no fertilisation in this area and management is aimed at soil impoverishment.

The experimental set-up was designed under the assumption that the desired lower availability of nutrients could be regenerated by using base-rich groundwater to raise the groundwater level. The experimental area was set out in 1986: three hydrological compartments were installed (Figure 1). In the compartment with subsurface irrigation, artesian groundwater from the third aquifer at a depth of 50 m was infiltrated into the plots via a ditch and drains about 50 cm underground. Bringing base-rich water to just under the ground level like this mimics the effect of seepage. In another compartment, only precipitation was conserved. Here, dams were installed in the ditches at a height of c. 10 cm below ground level. The control compartment had no hydrological measures. Various management measures were applied in each hydrological compartment: an area was extensively grazed and trial plots were laid out in quintuplicate to study the effect of different ways of mowing and sod-stripping.

The monitoring study entailed:

a: frequently recording control variables deemed to be important, at three supposedly typical measuring locations.

b: pedological study in the compartments once every four years, to investigate certain soil properties thought to be important (Kemmers et al. 1995).

The recording (see (a) above) entailed measuring the groundwater levels in the uppermost aquifer intensively (4 times an hour, using a data recorder) from 1986 onwards. The groundwater levels in the intermediate and deep aquifers were measured manually twice monthly. The groundwater quality in the root zone (at depths of 10, 30 and 60 cm) was determined annually at these sites three times a year from 1989. The parameters measured were: pH, EC 20 ºC, major ions (Na^+, K^+, Ca^{2+}, Mg^{2+}, HCO_3^-, SO_4^{2-}, Cl^-), NO_3^-, NH_4^+, PO_4^{3-}, $Fe^{2+/3+}$, Al^{3+}. In this contribution, only the calcium content of the groundwater will be discussed. The water types present have been described in detail in Schouwenberg et al. (1991). The influence of groundwater level management on the soil chemistry was monitored from 1988 onwards by measuring the redox potential in duplicate twice a month at depths of 5, 15, 40 and 60 cm in the same place where the groundwater levels were measured.

The pedological study entailed doing comparative studies in October 1986, 1989, 1991, 1993 and 1997. For this, a compound sample (0-10 cm depth) was prepared per compartment from 5 plots with the management regime ‘mowing + removal of the hay’. From these sample the following were determined: % organic matter, pH-KCl, %C, %N, total P (determined using P_{+ox}), inorganic P (determined using P_{-ox}), available P (calculated from the Pw value), bulk weight, CEC and base saturation.

In 1992, in response to the preliminary results of the monitoring, further research was done on the phosphate availability in De Veenkampen (Nap 1993). Five compound samples, each consisting of five subsamples, were taken in the compartments, at four depths below the ground level (0-5 cm, 10-15 cm, 15-20 cm and 30-35 cm). These samples were first used to characterise the present state of the availability of P in De Veenkampen. The following were determined: pH-H_2O, the desorption of phosphate (using filter paper impregnated with aluminium oxide, in accordance with Sharpley, 1991) and the sorption capacity of the soil (oxalate-extractable amounts of iron and aluminium). Next, two shaking experiments investigated the reaction of phosphate with the soil. Only the uppermost 5 cm of soil was studied, because this layer is the most important for the amount of available P.

The adsorption of the soil was studied by shaking the soil at a pH of 5.5 with phosphate solutions (NaH_2PO_4 0.01 M) of five strengths and by measuring the amount of P adsorbed and the P content of soil moisture after 20 hours (standard adsorption time). In one experiment the adsorption kinetics of soils from all three compartments was determined in this way. In the other experiment the dependence of the phosphate sorption on the calcium concentration of the solution was studied by subjecting the soil to three $CaCl_2$ concentrations: 0.1 M, 0.01 M and 0.001 M. The latter experiment was conducted solely using soil from the compartment with years of subsurface irrigation, because it was expected that the hydrological management here would have the clearest impacts on the phosphate availability.

The reference

When designing the experimental set-up it was attempted to create the most favourable conditions possible for the restoration of wet, nutrient-poor grasslands. These conditions were derived from hydrological and vegetation science data from the 1940s and from research in the nearby Bennekomse Meent nature reserve. The old vegetation surveys of De Veenkampen and surroundings reveal that orchid-rich litter meadow occurred. At that time the dry matter yield of De Veenkampen was 4.5 - 5.5 ton/ha and the N, P and K contents in the crop were respectively 2 - 2.3, 0.15 - 0.22, 1.7 - 2.2 % (Oomes et al. 1998). In winter, the area was typically inundated as a result of percolation of seepage water, and the soil was peaty (van der Schaaf 1998).

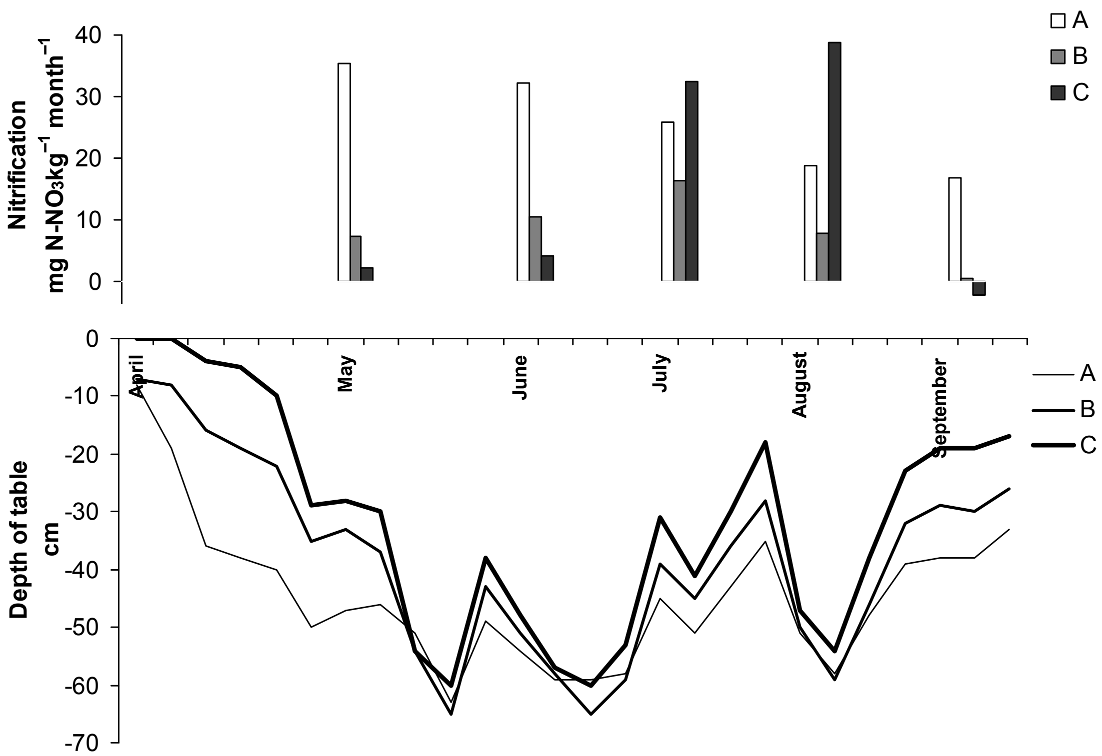

Figure 3. Depth to groundwater (cm) and net nitrification (mg $N\text{-}NO_3$ kg^{-1} $month^{-1}$) at three hydrologically different sites (A, B and C) of a *Cirsio-Molinietum* ecosystem in the Bennekomse Meent.

In the Bennekomse Meent nature reserve that lies 2 km north of De Veenkampen there is still c. 7 ha of litter meadow. Peaty and peaty sandy soils occur, with upward seepage of groundwater locally reaching the surface. At three hydrologically different locations in this nature reserve research was done on the specific hydrological requirements of species-rich, nutrient-poor grasslands (Van der Hoek & Braakhekke 1998). In the centre of the reserve the soil is peaty, with a sandy subsoil at a depth of 1 m. Here, the base-rich groundwater reaches the root zone. The greatest cover here is from carnation sedge (*Carex panicea*), tawny sedge (*Carex hostiana*), purple moor-grass (*Molinia caerula*) and meadow thistle (*Cirsium dissectum*), and rare species such as flea sedge (*Carex pulicaris*) and marsh gentian (*Gentiana pneumonathe*) are present in large numbers. In the past fifty years there have been few if any changes in the species composition and cover at this location. The reserve's border zone is influenced by the effects of drainage and by the inflow of nutrients (Van der Hoek & Van der Schaaf 1988). The draw-down has resulted in an increase of species here, such as sweet vernal grass (*Anthoxantum odoratum*), heath grass (*Danthonia decumbens*), red fescue (*Festuca rubra*) and sheep fescue (*Festuca ovina*). The eutrophication has brought about a decline in carnation sedge, tawny sedge, meadow thistle and marsh gentian and an increase in Yorkshire fog (*Holcus lanatus*), ribwort plantain (*Plantago lanceolata*) and meadowsweet (*Filipendula ulmaria*). Van der Hoek & Braakhekke (1998) demonstrated that in this litter meadow there was a positive correlation between the depth to the groundwater and nitrification: the shallow groundwater levels at the start of the growing season, which are characteristic of the presence of upward seepage, are associated with low nitrification. In places with litter meadow plant communities suffering from the effects of drainage the groundwater level falls early in spring, and at the start of the growing season a relatively strong nitrification can already be measured (Figure 3). The study elucidated the phosphorus cycle and the significance of the level and quality of the groundwater for the availability of P. The latter is of enormous importance for the biomass production and species composition of a litter meadow (Pegtel *et al.*, 1996). The total phosphate reserves in the topsoil were found to be appreciable (1500 kg ha^{-1}, 20 cm depth), which is more than 100 times the amount occurring in the crop and litter. An important part (85%) of this is organic phosphate; under the prevailing high groundwater levels little of this is converted into forms of P the plants can take up. The reserves of inorganic phosphate (15% of the total P) are about 200 kg ha^{-1}, 20 cm depth. In the event of acidification, much P could be released from this inorganic fraction. The presence of base-rich groundwater in the root zone, however, ensures a large acid buffer capacity, as a result of which the pH remains at a level of 5.5. Since little phosphate that could be bonded to soil particles (adsorption) is released from the organic matter on a yearly basis by mineralisation (decomposition), and because this desorption is limited, the phosphate concentration in the soil solution remains low.

The most important conclusion from this benchmark study was that seepage of base-rich groundwater is indeed essential for the site properties that are characteristic of the litter meadow: high spring and summer groundwater levels, resulting in a low mineralisation of N and P, and a large buffer capacity against acidification in the root zone.

Trends in the steering process

It is being attempted to restore the high spring and summer groundwater levels and the buffer capacity of the soil in De Veenkampen by importing artesian groundwater. The conservation of precipitation is an alternative strategy that is often applied. When the research started, it was unclear how effective this measure directed at regeneration would be. Below, the following will be discussed: the levels and quality of groundwater achieved in De Veenkampen by both measures, and their significance for trends in the conversion processes in the soil.

Level and quality of groundwater

The effect of the hydrological measures is visible in the mean groundwater levels and in the annual fluctuations of groundwater levels. For example, in 1989 the groundwater level in the compartment with subsurface irrigation was clearly higher in spring and summer than in the other compartments; the latter show only small differences (Figure 4). In the subsurface irrigation treatment, the mean annual groundwater levels are always significantly higher than elsewhere (student's t test, $P < 0.001$). The same is true for the mean spring groundwater level. The mean groundwater levels in autumn and winter do not differ significantly between the compartment with subsurface irrigation and the compartment with conservation of precipitation; the differences between the compartment with subsurface irrigation and the control are significant ($P < 0.001$). Van der Schaaf (1998) has described the hydrological mechanism responsible for this result: in the environs of De Veenkampen and in the control plot the hydraulic head of the second aquifer is higher than that of the capping layer. In the compartment with conservation of precipitation, downward seepage dominates, but in summer weak upward seepage can occur, though this does not occur between the first aquifer and the capping layer. This means that the upward seepage does not reach the root zone. When water is supplied, there is only downward seepage; as a result of the infiltration the upward seepage becomes downward seepage.

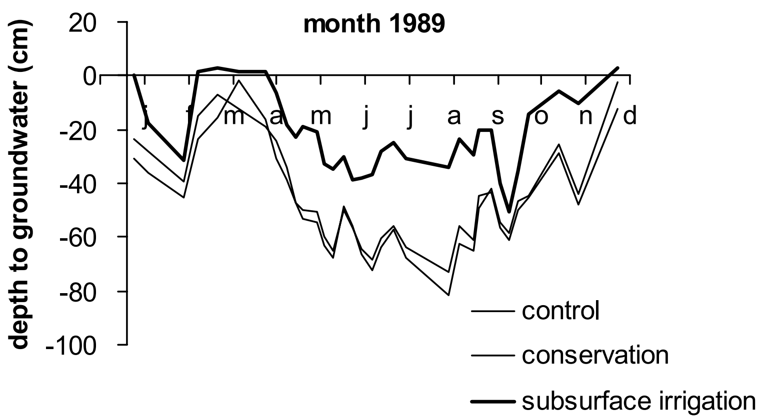

Figure 4. Depth to groundwater (cm) in 1989 in the control, in the compartment with conservation of precipitation and in the compartment with subsurface irrigation.

In each compartment, depending on the nature of the hydrological measures applied, a change has occurred in the groundwater quality over depth and over time. Schouwenberg et al. (1991) has given a picture of the mean chemical composition of the shallow groundwater during the period 1988-1990. In the compartment with subsurface irrigation the proportions of Ca^{2+} and HCO_3^- were found to be relatively large. In the compartment with conservation of precipitation, and to a lesser extent in the control, the proportion of SO_4^{2-} was large. The calcium content of the irrigated artesian water was only c. 10 mg l^{-1}, however. Because the measures were intended to recover the soil's buffer capacity by supplying base-rich groundwater, when the data on water quality were analysed particular attention was paid to trends in the calcium content of the groundwater over time and at different depths. This led to the results described below:

In the control compartment the calcium content at a depth of 10 cm was c. 40 mg l^{-1}. Higher values (up to 100 mg l^{-1}) were observed in the upper soil, particularly in the compartment with subsurface irrigation; however, over the years these concentrations declined. In all compartments, similar calcium contents were found at a depth of 30 cm; over the years these decreased slightly from 80 to 50 mg l^{-1}. It is striking (Figure 5) that in the subsurface irrigation treatment there were significantly lower contents (20 - 40 mg l^{-1}: Van Geer & Gieske 1995) at a depth of 60 cm below ground level than in the control compartment (50 - 80 mg l^{-1}). The calcium content of the (spring)water supplied remained fairly constant during the monitoring period and was only c. 10 mg l^{-1}.

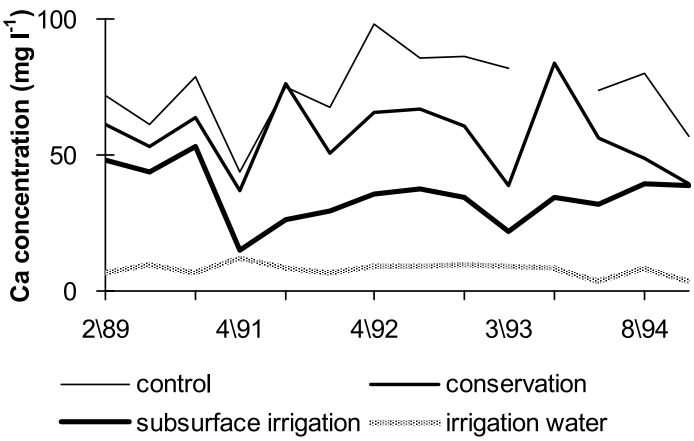

Figure 5. The calcium content (mg l^{-1}) of the soil solution at a depth of 60 cm in the control, in the compartment with conservation of precipitation and in the compartment with subsurface irrigation.

On the basis of these results it is possible to draw the following conclusions about the effectiveness of the hydrological measures:

- In all the compartments the precipitation penetrates the topsoil and this is accompanied by a fall in the calcium content. The outcome is the disappearance of the differences between the compartments that may be related to prior differences in fertilisation. This acidification has not yet penetrated to 30 cm depth, but it will probably soon do so.
- In the very wet and damp compartments, conserving precipitation by means of dams has led to a decline in the calcium content in the topsoil.
- Supplying groundwater relatively low in calcium at a depth of 50 cm has resulted in intensified calcium leaching from the subsoil.

Redox conditions

The redox potential indicates the extent to which oxidising or reducing conditions prevail in a soil. These conditions regulate the oxidisation of organic matter, the mineralisation of N and P and hence their availability for the vegetation (see Figure 2). During the oxidation and reduction processes, micro-organisms convert organic matter. The nature of the organic matter changes as a result of this process, with the result that ultimately only poorly decomposable organic compounds remain. If oxygen is available (aerobic conditions), the redox potential is above c. 300 mV and decomposition is brought about by obligate aerobic micro-organisms. If oxygen is lacking, nitrate functions as the oxidator of the organic matter and is thereby reduced. Below 200 mV there is usually no nitrate found in the soil and there is relatively slow anaerobic decomposition in which Fe^{3+} is reduced to Fe^{2+}. The result is that the phosphate bound to the Fe^{3+} goes into solution and can become available for uptake by the vegetation.

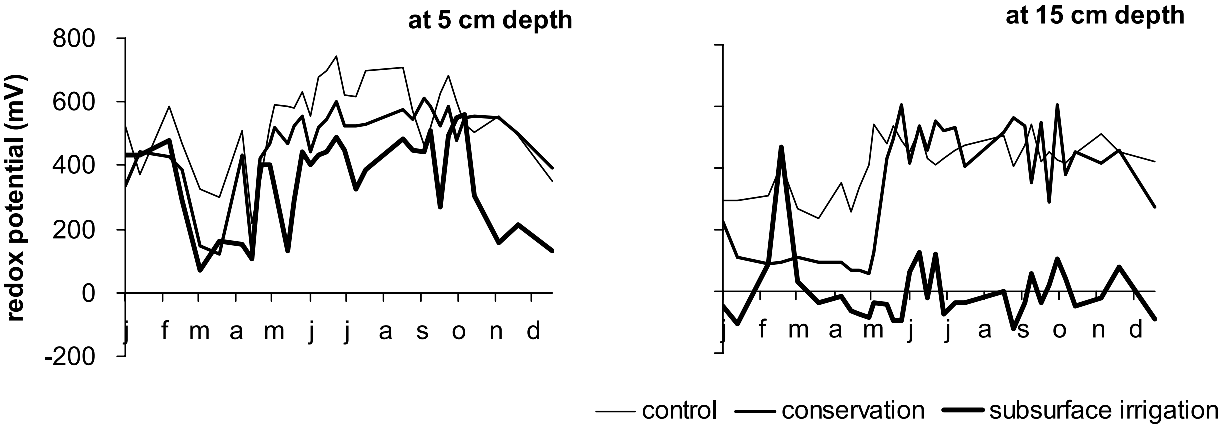

Figure 6. Redox potential (mV) during 1989 at depths of 5 and 15 cm in the control, in the compartment with conservation of precipitation and in the compartment with subsurface irrigation.

Figure 6 depicts the trends in the redox potential at depths of 5 and 15 cm during 1989. In the compartment with subsurface irrigation the redox potential at 15 cm depth was generally negative in the winter and spring. It exceeded the critical value of 300 mV only briefly. In this compartment the mean redox potential at depths of 5 and 15 cm in this and other years was significantly lower than in the other compartments (t-test, $P < 0.01$). In the compartment with conservation of precipitation and in the control, the critical value of 300 mV was exceeded for a long time at depths of 5 and 15 cm and nitrification could have occurred. At a depth of 5 cm the differences between the redox values in these two compartments were small. In all compartments, the redox potential at a depth of 5 cm decreased when the groundwater level rose and increased when the groundwater level fell (Spearman rank correlation test). In the compartment with conservation of precipitation and in the control, the redox potential at 15 cm depth was also inversely correlated with the height of the groundwater level. The reason that this relation was not found in the compartment with subsurface irrigation is because in that compartment the groundwater level was permanently high and anaerobic conditions therefore prevailed.

When all the data assembled per year were analysed, no clear linear relationship was found between the groundwater level and the redox potential. There was a demonstrable linear relationship between the groundwater level and the redox potential when the data collected during a long dry period were analysed. This was the case, for example, for the dry growing season (March to September) of 1989 for the redox values measured at 5 cm depth in all compartments (Figure 7). From this figure it is clear that the redox potentials measured at high groundwater levels in the compartment with conservation of precipitation and in the control fluctuated relatively greatly. In these compartments there were apparently periods in which the redox potential in the topsoil remained high during high groundwater levels. This phenomenon has also been reported by De Mars (1996) in drained carr peat areas. He argued that in spite of rising groundwater levels the expected fall in the redox potential in such soils cannot occur, because the degraded quality of the organic matter makes it impossible for reduction to take place.

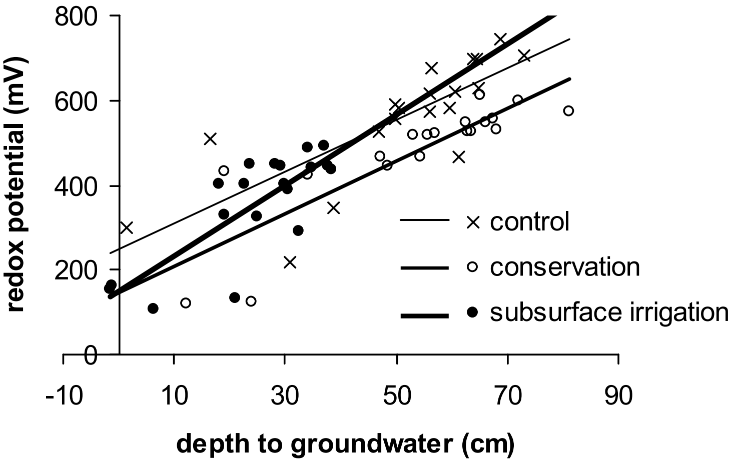

Figure 7. Relation between redox potential (mV, at 5 cm depth) and depth to groundwater (cm) during a dry period in 1989 in the soil of the control, in the compartment with conservation of precipitation and in the compartment with subsurface irrigation; the linear fit R^2 is 0.61, 0.73 and 0.64, respectively.

Both in the compartment with conservation of precipitation and in the control there was also a linear relationship with the redox values from 15 cm deep. Here, a falling groundwater level was accompanied by deeper aeration. The rewetting achieved by supplying water did indeed influence the course of the mineralisation process in the topsoil, so that this began to show more similarities with the rhythm observed in the litter meadow grassland of the reference area, but the amount of nitrogen made available in the growing season remained appreciable.

Trends in available nutrients as a result of rewetting

As it was anticipated that the water management implemented would have an effect on the nitrogen cycle, research was initially done on the correlation between the groundwater level, the redox potential and the nitrogen mineralisation. During the period from March 1988 to March 1989 the nitrogen mineralisation was measured by the AB-DLO research institute, by means of field incubation. The annual mean mineralisation

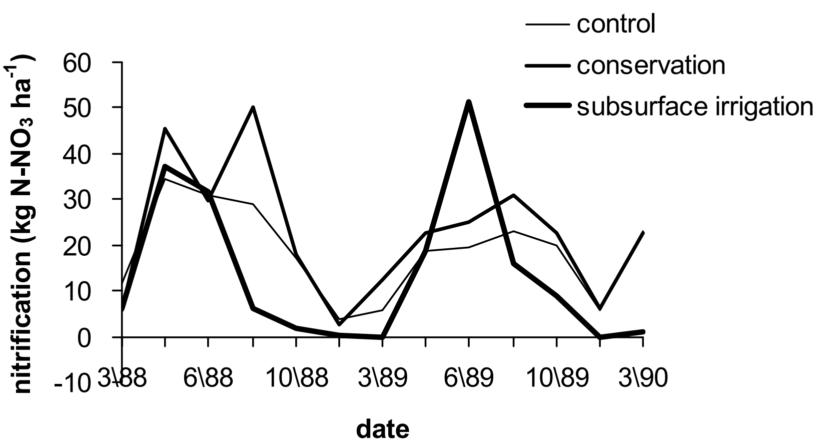

Figure 8. Net nitrification (mg N-NO_3 kg^{-1} month^{-1}) in 1998-1990 in the topsoil of the control,of the compartment with conservation of precipitation and of the compartment with subsurface irrigation.

(ammonification+nitrification) was 211 kg ha^{-1} in the compartment with subsurface irrigation and 159 kg ha^{-1} in the control (Berendse et al. 1994). From the data available it was clear that the within-year fluctuations in the nitrification were large, especially in the compartments with subsurface irrigation and conservation (Figure 8).

In the compartment with subsurface irrigation, there was zero nitrification in the winter period. It is striking that in all compartments there was a linear relation between the nitrogen mineralisation, particularly the nitrification, and the groundwater level (Figure 9). In addition, for all the compartments a positive rank correlation was found between the nitrification and the redox potential. Only in the control was a linear relation (weak) found between these variables. Given the high redox potentials measured at 40 cm depth in the control, it can be expected that in this compartment the aeration penetrates deeply as a result of the falling groundwater level and that nitrification will also occur in the subsoil. This phenomenon is much less marked in the compartment with conservation of precipitation.

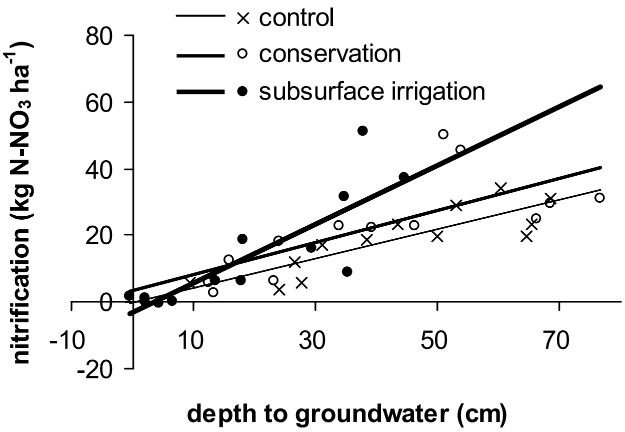

Figure 9. Relation between net nitrification (kg N-NO_3 ha^{-1}) in the topsoil and depth to groundwater (cm) in the control, in the compartment with conservation of precipitation and in the compartment with subsurface irrigation; the linear fit R^2 is 0.72, 0.54 and 0.76, respectively.

To obtain an overall picture of the effectiveness of 10 years' rewetting, the relative increase or decrease of certain soil properties was calculated. This change was calculated in relation to the starting situation and the autonomous changes that occurred in the control. Using this method, the differences between the three compartments in the initial situation (1986) were determined per variable, and were set at 100% per variable. In addition, the trend in the control was eliminated by constantly resetting the value at 100%. The calculation method was:

$M\text{-effect}_{var.x} = (M\text{-Obs.}_{var.x} \ / \ M.Exp._{var.x}) * 100$

$M\text{-Exp.}_{var.x} = M\text{-Obs.}_{var.86} * (C\text{-Obs.}_{var.x} \ / \ C\text{-Obs.}_{var.86})$.

$M\text{-effect}_{var.x}$: the relative effect of a measure on a variable in a given year (x) in %

$M\text{-Obs.}_{var.x}$: the absolute value of a variable, measured after the implementation of a measure, in a given year (x)

$M\text{-Exp.}_{var.x}$: the expected value of a variable after the implementation of a measure, in a given year (x)

$C\text{-Obs.}_{var.86}$: the absolute value of a variable, measured in the control in 1986

$C\text{-Obs.}_{var.x}$: the absolute value of a variable, measured in the control in a given year (x)

The effect of rewetting calculated in this way can be seen in Table 1: a percentage higher/lower than 100 shows whether the value of a variable in the compartment concerned has increased/decreased *vis-à-vis* the control in the period indicated. This comparative method shed light on the repercussions of rewetting on the buffer capacity, the organic matter and the reserves and availability of nutrients in the topsoil.

Table 1. Changes in soil parameters (0-10 cm depth) relative to the control (=100%) as a result of conservation of precipitation and subsurface irrigation.

	Compartment	1986	1989	1991	1993	1997
Ca/CEC	Conservation	100	101	94	95	90
%	S.surface irrig.	100	94	90	98	98
Exch. Ca	Conservation	100	114	103	95	89
kg ha^{-1}	S.surface irrig.	100	98	86	96	91
H/Ca ratio	Conservation	100	96	123	118	135
	S.surface irrig.	100	120	141	114	114
OM	Conservation	100	91	89	98	97
kg ha^{-1}	S.surface irrig.	100	102	107	105	106
Total N	Conservation	100	105	104	95	95
kg ha^{-1}	S.surface irrig.	100	112	105	101	107
Total P	Conservation	100	105	120	108	108
kg ha^{-1}	S.surface irrig.	100	87	86	86	95
inorg. P	Conservation	100	118	119	124	121
kg ha^{-1}	S.surface irrig.	100	81	75	85	89
Available P	Conservation	100	169	132	135	141
mmol P m^{-3}	S.surface irrig.	100	69	56	46	46
C:N ratio	Conservation	100	106	99	109	105
	S.surface irrig.	100	127	92	112	107
C:P ratio	Conservation	100	118	87	109	102
	S.surface irrig.	100	144	104	132	117

In the topsoil of both compartments the buffer capacity (measured from the amount of exchangeable calcium) and the calculated Ca saturation of the adsorption complex appear to decline somewhat. This decline seems to be sharper for the conservation of precipitation than for subsurface irrigation. In agreement with this is the fairly sharp increase that has occurred in the ratio between exchangeable H^{+}/Ca^{2+}, particularly in the compartment with conservation of precipitation.

The amount of organic matter in the topsoil has increased in the compartment with subsurface irrigation and has barely decreased in the compartment with conservation of precipitation. When conditions were very wet in the subsurface irrigation treatment, there was some increase in the C:N quotient and a sharp increase in the C:P ratio. This increase was not so sharp with conservation of precipitation, suggesting that the organic matter is being enriched by material with high C:N and C:P ratios .

In the compartment with subsurface irrigation the N reserves appear to increase; with precipitation conservation they appear to decrease somewhat. The opposite is the case for the P reserves. It seems that intense rewetting leads to the accumulation of nitrogen and the loss of phosphorus. Phosphate loss seems primarily attributable to the depletion of the reserves of inorganic P. The decline in the P concentration in the soil moisture (available P) under reducing conditions (see Figure 6) in the compartment with subsurface irrigation is very striking. By contrast, under the less wet aerobic conditions prevailing in the other compartment, P seems to accumulate in inorganic form. The higher P concentrations here are probably the result of an equilibrium reaction with the inorganically bound phosphorus. The conclusion from this study is that in De Veenkampen the rewetting achieved by supplying water has not achieved the desired effect: it has led to slight acidification instead of the desired buffering, but on the other hand it has led to a loss of phosphorus and lower P concentrations in the soil moisture and, moreover, to the build-up of organic matter primarily comprised of still scarcely broken down organic matter.

The key process: regulating the availability of P

Although since 1978 the management of De Veenkampen has been aimed at impoverishment, there is still plenty of phosphate in the topsoil. The total amount of P in the soil is c. 720 kg ha^{-1} in the uppermost 10 cm; appreciable amounts will still be found at greater depths. Much (c. 310 kg) of the phosphate in the topsoil is present as inorganic P. Much phosphate is also present in the soil of the litter meadow of the Bennekomse Meent reference area, but the availability of P is low and the proportion of inorganic P is only 15%.

The question was: how can the phosphate in the soil of De Veenkampen be made available, and what influence have the hydrological measures implemented had, or may still have, on this?

Acidity and P precipitation

The soil pH is an important control variable for the phosphorus cycle in the soil. Table 2 shows that in all compartments the pH-H_2O increases with depth. Everywhere, some acidification has occurred in the topmost layer as a result of the downward seepage of the precipitation. In both rewetting compartments the pH measured at 15 - 35 cm depth is significantly lower than the control. In the compartment with subsurface irrigation this is also the case for the 10 - 15 cm layer. It can be concluded that under the prevailing pH values there will be no solution and precipitation phenomena of calcium phosphates (Janssen &Van Beusichem 1990). Thus, the measures implemented have worked counter to what was expected.

Table 2. pH-H_2O at various depths (cm) in the three compartments (means ± SD) .

Depth cm	Subsurface irrigation	Conservation of precipitation	Control
0-5	5.38 ± 0.12	5.44 ± 0.08	5.43 ± 0.12
10-15	5.52 ± 0.04	5.58 ± 0.17	5.73 ± 0.12
15-20	5.67 ± 0.12	5.66 ± 0.15	5.96 ± 0.05
30-35	5.96 ± 0.06	5.93 ± 0.07	6.20 ± 0.09

P adsorption

The availability of phosphate is primarily dependent on the adsorption and desorption behaviour of iron and aluminium compounds. Table 3 illustrates that the amounts of oxalate-extractable iron (Fe-oxal.) and aluminium (Al-oxal.) in the topsoil are large, which has to do with the high content of organic matter and clay. These are reactive amorphous oxides and hydroxides of iron and aluminium to which inorganic P (P-oxal.) is fixed, primarily by adsorption. P-oxal. is lower in the very wet and damp compartment than in the control compartment. In all compartments a decline of P-oxal. with depth can be seen.

The P in De Veenkampen removed with the hay is c. 14, 10 and 13 kg ha^{-1} yr^{-1} in the compartment with subsurface irrigation, conservation of precipitation and the control, respectively (Oomes et al. 1998). It can be concluded that the measure of mowing and removal, through which no more than 1% of the adsorbed P (P-oxal.) is removed per annum, has no major influence on the phosphate balance.

Table 3. Fe, Al and P (µmol g^{-1}) extracted by oxalic acid at various depths (cm) from the three compartments (means ± SD).

	Subsurface irrigation			**Conservation of precipitation**			**Control**		
Depth	**Fe-oxal.**	**Al-oxal.**	**P-oxal.**	**Fe-oxal.**	**Al-oxal.**	**P-oxal.**	**Fe-oxal.**	**Al-oxal.**	**P-oxal.**
0-5	147 ± 33	174 ± 1	20 ± 0.7	142 ± 1	160 ± 4	21 ± 1.4	162 ± 1	168 ± 3	30 ± 0
10-15	135 ± 1	179 ± 6	18 ± 0.7	160 ± 2	174 ± 1	19 ± 0.7	149 ± 9	160 ± 25	23 ± 3.5
15-20	138 ± 4	189 ± 4	15 ± 1.4	135 ± 5	189 ± 4	15 ± 1.4	116 ± 13	180 ± 2	18 ± 0.7
30-35	45 ± 11	178 ± 1	9 ± 1.4	51 ± 14	197 ± 21	13 ± 0.0	57 ± 24	211 ± 13	17 ± 0.7

P desorption

The phosphate concentration in the soil solutions was generally low (0.01 - 0.15 mg l^{-1}). As plants can lower the P concentration in the soil solution to almost zero, it is important to know what part of the soil phosphate can be delivered later to the soil solution and in what amounts.

Table 4. Average P desorption (Pi) in µmol g^{-1} (means ± SD), at various depths (cm) in the three compartments.

Depth cm	**Subsurface irrigation**	**Conservation of precipitation**	**Control**
0-5	0.52 ± 0.1	0.51 ± 0.2	0.51 ± 0.2
10-15	0.59 ± 0.2	0.37 ± 0.2	0.45 ± 0.2
15-20	0.43 ± 0.1	0.21 ± 0.0	0.33 ± 0.1
30-35	0.48 ± 0.1	0.21 ± 0.0	0.18 ± 0.0

Table 4 shows the desorption of phosphate (Pi) measured using filter paper impregnated with aluminium oxide. The desorption is low: around 0.5 µmol g^{-1} in the topmost layer. Therefore only a small proportion of the amount adsorbed is liberated (P-oxal.: 20-30 µmol g^{-1}). At all depths in the compartment with subsurface irrigation, except for the top layer, the Pi values are much higher than in the other compartments. Because the amount of phosphate sorbed to the soil particles (P-oxal.) declined with depth it was expected that the desorption would decrease with depth. This appeared to be the case in the compartment with conservation of precipitation and in the control, but in the compartment with subsurface irrigation, the Pi remained around 0.5 µmol/g, even at greater depths. The greater phosphate desorption in the compartment with subsurface irrigation seems to be caused by the wet anaerobic conditions prevailing there, under which phosphates, including iron phosphate, go into solution. Grootjans (1985) has also reported this phenomenon.

To obtain more insight into the question of what operational significance the rewetting has had or could have for the availability of phosphate, two adsorption experiments with soil were performed.

P adsorption experiments

Figure 10 shows the adsorption values of the soil samples from the compartments at t=20 h (standard adsorption time), after intensive contact with phosphate solutions with increasing concentrations. The adsorption was greatest in the compartment with subsurface irrigation, followed by the compartment with conservation of precipitation; the soil from the control adsorbed the least.

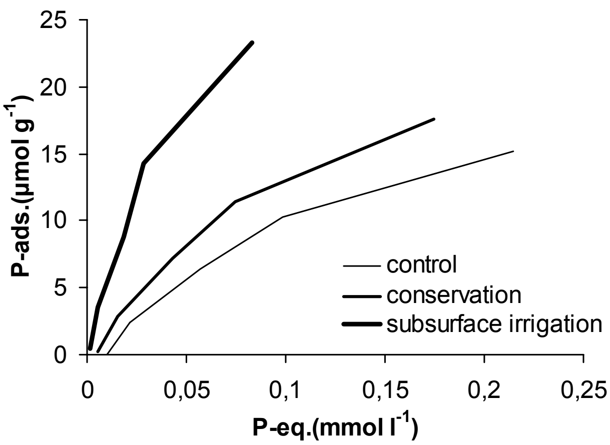

Figure 10. P adsorption (µmol g^{-1}) in the soil (0-5 cm depth) related to the P concentration (mmol l^{-1}) in the soil solution (P-eq) of the three compartments after 20 hours of intensive contact with phosphate solutions, NaH_2PO_4 at five concentrations.

The greater adsorption in the compartment with subsurface irrigation is probably caused by the higher organic matter content. If rewetting continues, this bonding could become still more important as a result of the increase in the amount of organic matter.

To ascertain the influence of the calcium concentration of the soil moisture on the adsorption behaviour of phosphate in the soil, an analogous experiment was performed in which soil from the compartment with subsurface irrigation was shaken with three $CaCl_2$ concentrations. Figure 11 shows the relation between the P content in the soil moisture and the amount of P adsorbed, for each of the solutions. Under the current situation in De Veenkampen, which is characterised by a low concentration of P in the groundwater, the line for 0.001M $CaCl_2$ is applicable. It is clear that P adsorption will only rise appreciably if the calcium content of the groundwater increases by a factor of 10 or more, so that the line for 0.01 becomes applicable. Under the current hydrological conditions in De Veenkampen this will never occur because the calcium content of the deep groundwater is much too low.

The monitoring study showed that the opposite development has occurred: since 1986 the calcium content of the groundwater has declined and the subsurface irrigation has actually increased the leaching out of the calcium in the subsoil. The only way to obtain a high calcium content in the groundwater is to lime or to use base-rich surface water.

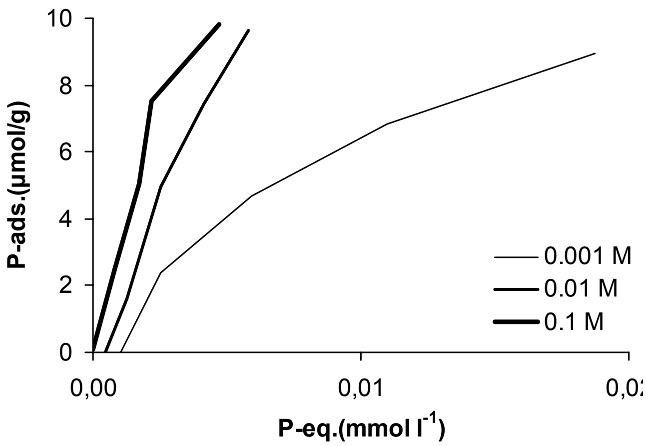

Figure 11. P adsorption (µmol g^{-1}) of the soil from the compartment with subsurface irrigation, at three $CaCl_2$ solutions (0.1M, 0.01 M and 0.001 M), related to the P concentration (mmol l^{-1}) in the soil solution (P-eq), after 20 hours intensive contact with phosphate solutions, NaH_2PO_4 at five concentrations.

Conclusion

The soil study in the trial plots in De Veenkampen has elucidated the effect of rewetting on regeneration processes in a clayey peat soil.

Rewetting in De Veenkampen by supplying water has brought about high spring groundwater levels, leaching and, in the longer term, a superficial acidification. This has repercussions for the development of the organic matter in the soil. The organic matter content is increasing under the influence of rewetting, while the proportion of labile humus becomes larger.

As a result of this rewetting method, short dry periods are alternating with long, wet periods. As a result, the N mineralisation begins late in the year and the amount of available phosphate is decreased. The latter result is associated with the occurrence of the following physico-chemical and biological processes in the soil: under the dry conditions the organic matter decomposes, resulting in the occurrence of the mobilisation of nitrogen and phosphate; in the aerobic environment the phosphate is then bound to Fe^{3+} compounds. During the dominant wet periods the reserves of organic matter are built up under the influence of the anaerobic conditions and the Fe^{3+} compounds are reduced to highly soluble Fe^{2+} compounds. The consequence is that phosphate will dissolve in the soil solution and will disappear from the soil ecosystem by leaching. In view of the huge reserves of nitrogen and phosphate in the soil it is essential for the impoverishment that the summer groundwater level remains as high as possible.

Retaining precipitation (water conservation), e.g. by blocking the ditches, is in itself not effective; the spring groundwater levels are raised only slightly and the summer groundwater levels do not change at all. Implementing this measure will not diminish the available nutrients.

The intense rewetting that was possible to achieve in De Veenkampen by subsurface irrigation will not lead to the recovery of the site properties that are characteristic of the orchid-rich litter meadow of yesteryear. The groundwater levels required can indeed be achieved by supplying water, but the deep groundwater that infiltrates via drains and ditches will not reach the root zone and, moreover, is insufficiently rich in bases, thus bringing about weakly acid conditions. A promising alternative is to reintroduce occasional inundations with base-rich surface water.

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7

General discussion

The aim of this study was to investigate the mechanisms that control the effectiveness of measures aiming at restoring species-rich fen meadows. In order to judge the sustainability of the success of measures that have been taken, in this final chapter I will discuss the recovery of resilience mechanisms in fen meadow ecosystems. The discussion will focus on acid buffering, nutrient availability and the persistence of re-established species. According to the hierarchical structure of the ecohydrological concept, resilience mechanisms may work at different levels that correspond to the scales of conditional and operational factors. Attention will be given to both levels of resilience in turn.

To gain insight into the resilience of fen meadows in undisturbed conditions I will first describe the resilience in relation to external hydrological conditions in a semi-natural landscape. Subsequently, I will evaluate results of the study on the response of fen meadows to changes in hydrological conditions. Finally, I will discuss the effectiveness of restoration measures.

The functioning of an original, undisturbed fen-meadow ecosystem

The fen meadows I investigated are situated in nature reserves of brook valleys, which are characterised by upward seepage of deep groundwater. They are all relics of a former semi-natural landscape. In the past, acidophilous plant communities covered the higher parts of the landscape, whereas *Cirsio-Molinietum* fen meadows occurred down-slope. Mesotrophic hay meadows (*Calthion palustris*) or small sedge communities (*Parvocaricetea*) were found in low areas where prolonged inundation with groundwater or rainwater occurred. The variation in vegetation composition along the gradient reflected the corresponding gradients in hydrology and soil fertility. The nutrient gradients were very stable until the 20th century, when the regional and local hydrological systems were severely disturbed by drainage and fertilisation (Grootjans et al. 2002). According to Jansen et al. (2000), in my fieldwork areas these stable site conditions depended on base-rich groundwater, discharging from large groundwater systems.

The stable site conditions of the fen meadows in the southern part of the Gelderse Vallei are provided by discharge of base-rich water from deep aquifers. The groundwater in the deepest aquifer is mainly supplied by infiltration in the ice-pushed ridge of the Veluwe to the east. A piezometric level of 2-3 m above soil surface and a subsequent exfiltration of 1 mm d^{-1} were maintained at least until the first half of the 20th century (Van der Schaaf 1998). The upward seepage from this aquifer, together with local systems of infiltration and exfiltration in the upper and middle aquifers, sustained a constant upward discharge of groundwater into the root zone, which resulted in high groundwater levels and inundation along the brooks during the year (Bier et al. 1992; Van der Hoek & Van der Schaaf 1988).

Due to the mineral composition of the aquifers the concentrations of dissolved compounds in groundwater have always been relatively low (mean calcium concentration of 15-50 mg l^{-1} in the middle aquifer, according to Bier et al. 1992). The fen meadow of the Korenburgerveen also developed under the influence of the upward seepage of base-rich groundwater (calcium concentration of 100-150 mg l^{-1}, according to Van der Hoek & Van Walsem 2004) until the first half of the 20^{th} century, but here the hydrological system was smaller (De Meij 1999; Van der Veen 1998).

As a consequence of the hydrological position of the fen meadow sites, the concentrations of available nutrients and of protons were buffered at a low level by the stable high groundwater level and groundwater chemistry. These buffer mechanisms resulted in the fen meadows being very resilient to changes effected by fluctuations in hydrology. When I examined the buffering of changes in N availability, I found that extra N supplied may disappear because of immobilisation in the soil and increased denitrification, if it is present as nitrate (Chapter 3). Normally, however, the N output by denitrification is relatively low in unfertilised fen meadows (Berendse et al. 1994), due to limitation of nitrification by high groundwater levels, such as those I found at our typical *Cirsio-Molinietum* sites (Chapter 4, Nieuwenburg et al. unpublished). With regard to the buffering of the low concentration of phosphate in the soil solution, it was inferred that the net flux of phosphate into the soil solution is determined by decomposition of soil organic matter. However, the turnover of the large pool of organic P is very slow as a consequence of high groundwater levels. In addition, I assumed that desorption of labile, inorganic P and dissolution of P compounds are low because the pH is buffered at a neutral level (Chapter 4) and therefore any extra P supplied was soon removed from the soil solution by adsorption to iron oxides and hydroxides and organic matter (Chapter 3). This would explain why low availability of P could persist in undisturbed fen meadows. I conclude in Chapter 3 that small fluctuations in nutrient availability are buffered due to the site's specific hydrological conditions. Thanks to these resilience mechanisms, and due to the low input of N and P, nutrient-poor conditions could persist in undisturbed fen meadows. In addition, regular haymaking appears to be important in stabilising the nutrient-poor conditions, because it compensates efficiently for external nutrient inputs, especially since the rate of nutrient removal increases concomitantly with biomass production.

The acid–base status of undisturbed *Cirsio-Molinietum* sites depends primarily on the extent of external alkalinisation brought about by groundwater discharge of calcium and bicarbonate ions (Wassen 1990; Van Diggelen et al. 1994; Jansen et al. 2000). The consequent buffering of the neutral pH is predominantly sustained by cation exchange from the adsorption complex in the soil. Secondly, the acid–base status depends on the association of bicarbonate and therefore on the capacity to generate internal alkalinity upon reduction. This capacity is brought about by high groundwater levels and the presence of some nitrate and sufficient iron oxides (Chapter 5; Lamers et al. 1999, Kemmers et al. 2003). Both mechanisms result in undisturbed fen meadow soils having a high base status, particularly as proton production is low due to nitrification being limited in undisturbed fen meadow sites. I found a 60 – 80 % calcium saturation of CEC and pH-H_2O values up to 6 in soils of little disturbed reference sites in the fen meadows investigated (Chapters 3 and 5; Alterra 1999) and a relatively high mean acid-neutralising capacity (ANC, Figure 1).

The second-level resilience, which builds on the operational environment of an undisturbed fen meadow site, includes a characteristic internal nutrient cycling. This nutrient cycling is conditioned by low availability of nutrients (P, K and N) and by the species composition of the vegetation. Fertilisation experiments have shown that P generally limits the biomass production of *Junco-Molinion* stands up to 5 ton ha^{-1} (Egloff

1983; Pegtel et al. 1996; De Mars 1996; Güsewell et al. 2002). This agrees with the results of my fertilisation experiment (Chapter 3) and synecological study (Chapter 2). Even potassium may become in short supply after haymaking for many years, especially in high-lying drained sites (Chapter 3; Kapfer 1994; Van Duren & Van Andel 1997). My finding that N is the primary limiting nutrient for biomass production in the wet sites of our fen meadows (small-sedge meadows) agrees with the results of Olde Venterink et al. (2001) and Van Duren et al. (1997). This low availability of nutrients favours slow- growing species that produce slowly decomposing litter which, consequently, keeps nutrient availability low (Berendse 1990, 1998). *Carex panicea* for example, is a slow-growing and stress-tolerant species (Grime et al. 1988) that is well equipped to take up P and is not hampered by a low P supply (Boeye et al. 1999). I found that the growth of *C. panicea* in our fen meadow was actually limited by N whereas *Holcus lanatus,* a fast-growing and more competitive species, was P-limited. Due to the effect of the dominating Carex species on the soil, nutrient-poor conditions could persist and competitive species, e.g. *H. lanatus*, remained scarce (Chapter 3). P availability had more impact on the species richness in *Junco-Molinion* communities than N availability.

From these findings, I conclude that fen meadow ecosystems in the semi-natural landscape are able to absorb small fluctuations in external conditions thanks to their hydrological position, the applied strategy of haymaking and the internal positive feedback between nutrient availability and species composition. Provided that these resilience mechanisms are not overloaded or disturbed, stable soil conditions may persist for a very long time, facilitating the development of a species-rich fen meadow vegetation.

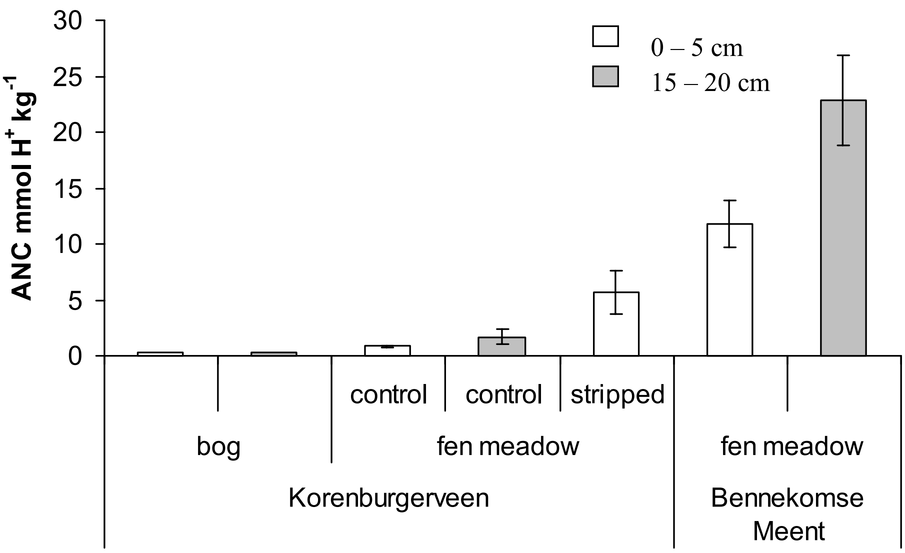
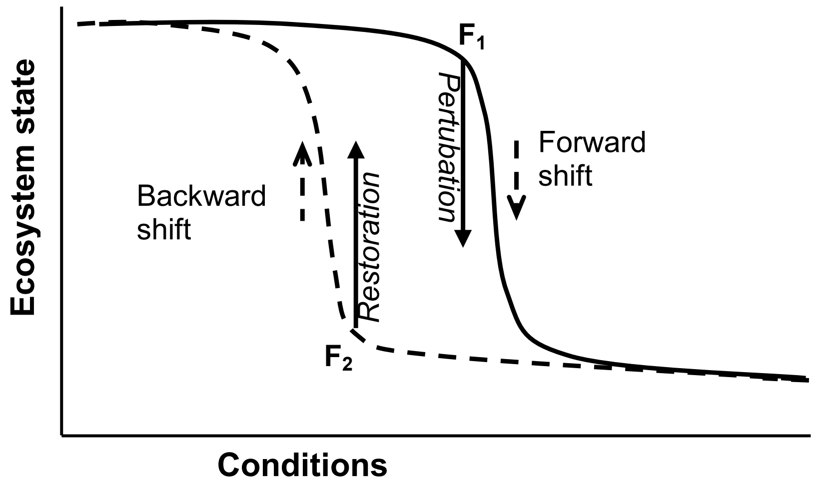


Figure 1. Acid-neutralising capacity (mmol kg^{-1} added H^{+} / mmol l^{-1} acitivity increase) at 0 – 5 cm and 15 – 20 cm depth, of the fen meadows in the Korenburgerveen and the Bennekomse Meent. Data compiled from Heijmans (1994) and Van der Hoek (2000).

The response of fen meadows to changes in hydrological conditions

Since the first half of the 20th century, the plant species diversity of fen meadow ecosystems in the Netherlands has drastically declined because of eutrophication and acidification. These processes have been triggered primarily by changes in hydrological conditions at regional and local scales, as a consequence of increased groundwater abstraction and the draining of fields for agriculture. In addition, increased atmospheric N deposition, large-scale reclamation and subsequent fertilisation have had overwhelming impacts. I found that a decrease in resilience, caused by changes in hydrology, may affect the species composition and aboveground biomass production of a fen meadow in different ways. These effects may be gradual, as in the Bennekomse Meent, or sudden, as in the Veenkampen. A sudden change in fen meadows may occur when conditions exceed critical levels. Scheffer et al. (2001) describe a "catastrophic shift" into an alternative stable state as a special case of a sudden change (box 1). Such a drastic shift, towards a plant community dominated by acidophilic mosses, was found in the Korenburgerveen fen meadow.



Box 1: Shifts between alternative stable states of an ecosystem.

An ecosystem may occur in alternative stable states (upper and lower parts), stabilised by biotic feedbacks. Shifts into a different state are triggered merely by physical events and may occur in the range of conditions between bifurcation points F_1 and F_2. When conditions are changed in the direction of F_1, a "catastrophic transition" to the lower state occurs (forward shift). In order to induce a switchback, it is not sufficient to restore the environmental conditions prevailing just before the collapse. Instead, one needs to go back beyond a second bifurcation point (F_2), where the system suddenly shifts to the higher state (backward shift). Perturbation and restoration may induce a shift to an alternative state, if changes in conditions exceed critical levels (modified from Scheffer et al. 2001).

Below I will discuss the gradual and sudden changes in fen meadows that I analysed in the fieldwork areas.

The gradual change of species composition in the Bennekomse Meent fen meadow was primarily caused by a decrease of the upward seepage. Hydrological modelling showed that groundwater extraction reduced the exfiltration rates in the Southern Gelderse Vallei basin by approximately 10% (Bier et al. 1992). Moreover, land reclamation in surrounding agricultural areas intensified the drainage and consequently, groundwater levels fell even deeper both outside and inside the reserves, especially in summer (Van der Hoek & Van der Schaaf 1988). The decrease of summer groundwater levels in the nature reserve after several consecutive dry summers shows the hydrological system's sensitivity to external changes. This decrease in summer levels is the combined effect of slightly reduced seepage and relatively high evapotranspiration (Van der Hoek & Van der Schaaf 1988).

The change in hydrology resulted in the disappearance of some plant species, such as *Parnassia palustris* (characteristic of wet and base-rich conditions) from the nature reserve, which suggests that the acid buffer capacity of the soil had dropped below a critical value (Figure 1). Plant species like *Plantago lanceolata*, *Anthoxantum odoratum* and *Holcus lanatus* increased during dry periods, which indicates increasing availability of nutrients (Van der Hoek & Van der Schaaf 1988). Nowadays, low groundwater levels are not longer restricted to periods with dry summers but have become permanent (Chapter 2).

Box 2: **Feedback mechanisms stimulated by changed conditions**

Positive feedback of eutrophication

When nutrient availability in grassland exceeds a certain threshold, this may trigger a positive feedback mechanism that accelerates eutrophication. When the aboveground biomass increases, the vegetation composition and characteristics of the dominant species will also change (Chapin 1980, Vitousek 1982), leading to dominance of species with high inherent maximum relative growth rates, low leaf lignin concentrations, short leaf longevity, and high biomass turn-over rates (Berendse 1990). As a consequence, more litter will be produced and the rates of litter decomposition and nutrient mineralisation will speed up (Van Vuuren et al. 1993, Berendse 1998). This may increase the nutrient availability to plants, reinforcing the initial increase in fertility.

Positive feedback of acidification in wet sites

Sphagnum species contribute to the acidification by active cation exchange and decreased decomposition rates due to the excretion of allelopathic monophenolics (Verhoeven & Liefveld 1997). The consequent depressed growth of vascular plants increases light availability and wetness, both of which feed back positively to the growth of *Sphagnum* (Van Breemen 1995). In addition, invading acidophilic *Sphagum spp.,* particularly, *Sphagnum palustre*, facilitate the increase of *Polytrichum commune* and both achieve a growing moss carpet (Bowden 1991; Paulissen 2004). Acidification is further stimulated by diminished surface runoff and more storage of precipitation water in the growing moss carpet.

In fen meadows these changes may take place after the influence of base-rich water in the topsoil has disappeared and the influence of rainwater has become dominant. Consequently, fen meadows may be acidified dependent on the acid buffer capacity of the soil (ANC), which in turn is related to the degree of Ca^{2+} saturation of the CEC. Normally, the CEC will be recharged with base cations from external sources and from reduction of iron oxides and sulphates (internal alkalinisation). However, if downward water fluxes dominate, leaching depletes iron oxides and the recharge of the CEC might be blocked (Kemmers et al. 2003). As a consequence, the vegetation will change into a *Parvocaricetae* community, with a different litter composition and less biological activity. The latter will lead to superficial organic horizons of dead roots in the soil (Van Delft et al. 1999; Van Delft et al. 2002). Due to the ongoing loss of ANC, the pH may drop from values of about 6.5 to 4, while moss species like *Sphagnum palustre, Polytrichum commune* will increase.

Nevertheless, I only found a gradual succession, which is according to Grootjans et al. 1986. This contradicts the assumption that draining a fen meadow causes internal eutrophication, due to increased mineralisation which may result in increasing biomass production (Vermeer & Berendse 1983; Vermeer & Verhoeven 1987; Bollens 2001; Boeye et al. 1999). In addition, this eutrophication might be stimulated by positive feedback (box 2).

I attribute the absence of such a catastrophic shift triggered by eutrophication in the Bennekomse Meent fen meadow to the internal biogeochemical processes in soil that buffer the effects of N and P pulses and keep N and P availability low (Chapters 3, 4). Furthermore, the hay removal strategy would have ensured that even though nutrient supply increased, extra nutrients continued to be removed.

Instead of a catastrophic shift towards productive, species-poor plant communities, the gradual change in hydrology and the consequent acidification resulted in a succession towards more acidophilous *Junco-Molinion* communities. This succession started in well-drained higher plots and continued in lower plots at the cost of *Calthion* species. The decline of the gradient was reduced by the higher acid-neutralising capacity due to the presence of more buffered groundwater at the lower end. Therefore I expect that the *Cirsio-Molinietum* will continue to exist in the Bennekomse Meent in spite of continuing acidification, although some migration of species to lower parts of the reserve may occur (Chapter 2).

On low, hardly drained plots of the Bennekomse Meent fen meadow, however, the succession towards *Parvocaricetea* communities might foreshadow a drastic shift caused by the increasing influence of rainwater (positive feedback of acidification in wet sites, box 2). Such a succession has occurred in the Korenburgerveen fen meadow (Chapter 5), where the upward seepage of base-rich groundwater into the root zone almost disappeared, even though high groundwater levels have been largely maintained by water conservation (Van der Hoek & Van Walsem 2004; Bell Hullenaar 2004). Due to the lowered pH and increased abundance of mosses and the acidifying effect of dominant mosses (box 2) the fen meadow vegetation in the Korenburgerveen has developed into a derivate community dominated by *Polytrichum commune*, while the Ca^{2+} saturation of the soil adsorption complex has fallen to less than 10 %. Consequently, the acid-neutralising capacity in the topsoil of the fen meadow has decreased, approaching the values in the neighbouring bog (Figure1). Strongly acidified, wet fen meadows (e.g. *Carici curtae-Agrostietum caninae*) occurring in sites where upward seepage had changed to downward recharge, have also been found by Kemmers et al. (2003). These authors conclude that such plant communities develop when the Ca^{2+} saturation of adsorption complex falls below 25 %, which is in accordance with the results reported in this thesis. However, they also found iron depletion by leaching and pH values that fell sharply to 3, which did not occur in the Korenburgerveen fen meadow where conditions (anaerobia and a sufficient redox capacity because of iron) favour internal alkalinisation (Chapter 5).

I conclude that a weakening upward seepage (due to drainage etc.), resulted in only a gradual shift in species composition in the Bennekomse Meent fen meadow, because buffer mechanisms and haymaking prevented a shift to an alternative stable state as a consequence of positive feedbacks from species characteristic for eutrophication or acidification (see boxes 1 and 2). The gradual shift in species composition was driven by acidification together with the presence of some upward seepage of base-rich groundwater, especially in low sites. In the Korenburgerveen fen meadows, the changes in plant communities have been more "catastrophic" at sites where the upward seepage has disappeared because, as a consequence of positive feedbacks, an alternative stable state of acidified and species-poor plant communities has developed there.

A drastic shift from fen meadows to species-poor plant communities due to drainage and fertilisation has occurred in agricultural areas, like the Veenkampen area, where the ditches drained the upward discharge of deep groundwater so that it could no longer reach the root zone. Forty years of fertilisation and water management with the resulting increased mineralisation, have led to the fields subsiding by 15-50 cm and the soil becoming eutrophied, with reduced organic matter content and pH of about 5.5. (Van der Schaaf 1998; Chapter 6; Oomes et al. 1996). The vegetation in the Veenkampen has changed from a species-rich *Cirsio-Molinietum* with aboveground biomass production of 3 to 3.5 ton ha^{-1} to species-poor grassland with a production of about 10 to 12 ton ha^{-1} (Oomes et al. 1996). This man-made shift in site conditions towards agricultural hayfields might be irreversible e.g. because the clay content has increased as a result of peat oxidation (Van der Schaaf 1998) and because of the disrupted balance between macro-nutrients in the soil (Oomes et al. 1998).

Restoration measures and their effectiveness

The aim of fen meadow restoration projects has been to restore the original state of a fen meadow, with its characteristic range of plant communities. These target plant communities, however, are associated with transitional phases in the succession that cover different time periods. The duration of these periods depends on the buffering of the specific site conditions against external factors and internal processes (Chapter 2). Therefore, the aim of restoration projects is to increase the duration of a transitional phase by realising the required environmental conditions, inclusive their characteristic fluctuations. There have probably always been shifts and fluctuations in *Junco-Molinion* target plant communities, in response to the former agricultural use.

A general conclusion of Jansen et al. (2000) and Grootjans et al. (2002) was that the success of fen meadow restoration measures depends on the hydrological system type and on the time that has elapsed since the degradation of the fen meadow. I have tried to unravel the processes that determine the effectiveness of restoration measures in fen meadows positioned in regional groundwater systems and influenced to a greater or lesser degree by upward seepage of groundwater. I hypothesised that gradual changes in fen meadows, as caused by eutrophication or acidification, are generally reversible, although restoration might be faced with hysteresis. Hysteresis means that the return to the original state is different from the forward shift after perturbation, and a large change in a control variable and time is needed to restore the original ecosystem (box 1). Drastic changes on the other hand, especially after a stable alternative state has developed (box 2), are expected to be irreversible, except when additional measures, such as turf stripping, are applied. Irreversibility means it is impossible to reverse the processes that have led to a new state after a change in the environment, even though control variables have recovered. This may be caused by an irreversible change in the soil as well as by a change in species composition in combination with the absence of seeds of the original species. Therefore, in this discussion special attention will be paid to the combined effects of hydrological measures and topsoil removal on the success of restoration management. Turfstripping and sod cutting has been involved in many restoration projects to remove acidified and/or eutrophied topsoil respectively, and to facilitate the recovery of soil conditions.

To investigate the mechanisms that control the effectiveness of measures for the restoration of species-rich fen meadows, three questions have to be answered which are related to the external conditions and the buffer mechanisms responsible for resilience. The first question (A) is to what extent the original hydrological system of fen meadows might be restored by hydrological measures. The fen meadows investigated in this research belong to large hydrological systems. Restoring these systems requires drastic measures in the regional water management and is often not a realistic option because of the far-reaching socio-economic consequences. The second question (B) is to what extent dependent factors (e.g. moisture, redox and pH) that affect nutrient cycling and base regulation might be influenced by restoration measures. The third question (C) is to what extent we may be able to restore target plant communities. It should be borne in mind that in addition to the required site conditions, the presence of a seed bank or seed dispersal of the target species is a precondition for the recovery of target communities. These aspects have not been investigated explicitly in this study.

These three questions will be discussed in the next section, in relation to hydrological measures carried out in the surroundings and within nature reserves (i.e. the infilling of ditches and conservation of precipitation) and removal of the topsoil (turf or sods). The effectiveness of restoration measures will be evaluated successively in the Bennekomse Meent, the Korenburgerveen and the Veenkampen, since this is the order in which a declining influence of upward seepage of groundwater was found.

With respect to the first question (A), about the extent to which the original hydrological system of fen meadows might be restored by hydrological measures: it is hardly possible to restore an entire regional hydrological system for the conservation of fen meadows in Dutch brook valleys. An exception is the Drentse Aa brook valley reserve, where a great part of the catchment area was rewetted successfully and target species reappeared within several years. These species re-established in sites where upward seepage of groundwater into the root zone had been restored and there had been little fertilisation before the start of the local restoration measures, which consisted of mowing without fertilisation (Grootjans et al. 2002). However, usually, the possibilities to restore regional hydrology are restricted and only local hydrological measures in the surroundings combined with measures within a reserve are realisable. In such cases, only if there is a strong discharge of base-rich groundwater from surviving deep aquifers can the upward seepage into the root zone be restored. Zeeman (1986) has shown that in such a situation it might be sufficient to restrict the draining of a bordering watercourse in order to restore the levels and chemical composition of the groundwater as well as the base status of the soil and to restore the vegetation, including target species such as *Cirsium dissectum* and *Carex pulicaris*.

In the Bennekomse Meent a moderately upward discharge of deep groundwater is still occurring, driven by infiltration in an extensive ice-pushed ridge. The infilling of ditches in the surroundings and the increased annual precipitation after the dry 1970s, have achieved locally higher groundwater levels in winter and spring (Bier et al. 1992). However, low groundwater levels in summer have generally persisted (Chapter 2). Monitoring the chemical composition of groundwater did not show the increase in upward seepage of base-rich groundwater into the root zone (Terlouw 2003) that hydrological modelling had predicted (Goossensen & Van der Hoek 1993). I conclude (Chapter 2) that the effect of the rewetting measures was insufficient to prevent infiltrating rainwater from acidifying the soil, especially in the high plots. Conservation of precipitation within the small nature reserve (13 ha) did not restore the higher ground water levels in summer that are necessary to supply the root zone with bases; instead, it only stimulated the acidification (Van der Hoek & Van der Schaaf 1988; Van der Schaaf 1998; Chapters 2, 6) – as described and predicted by modelling (Goossensen & Van der Hoek 1993).

The fen meadow of the Korenburgerveen developed under the influence of the upward seepage of base-rich groundwater, mainly supplied by infiltration in a nearby sandy ridge (De Meij 1999; Van der Veen 1998). However, the upward seepage of base-rich groundwater into the root zone had almost disappeared (Van der Veen 1998; Bell Hullenaar 2004) and calcium concentrations in the groundwater were gradually declining (Chapter 5). Hydrological modelling predicted that hydrological measures in the surroundings, such as the infilling of ditches, would be insufficient to restore the upward seepage of base-rich groundwater (Van der Veen 1998). Water conservation throughout the nature reserve (310 ha) increased the groundwater levels in the fen meadows throughout the year, but also strongly increased the influence of precipitation water at the cost of base-rich groundwater, which resulted in a thick moss carpet. Turf stripping, combined with some drainage, did stimulate the upward seepage of base-rich groundwater by promoting the superficial discharge of precipitation water (Chapter 5).

When upward discharge of deep groundwater into the root zone has disappeared, subterranean irrigation is not a successful restoration measure in small nature reserves, even when base-rich groundwater is used. Although it may raise groundwater levels, it stimulates downward seepage, as does water conservation, and will not prevent acidification of the topsoil. Such effects of underground irrigation with deep groundwater were found in the Veenkampen rewetting experiment (Chapter 6) and are attributable to the small size of the experimental field (13 ha). Hydrological models predict that the only way to achieve effective upward seepage in the Veenkampen is to enlarge its size tenfold (Van der Schaaf 1998).

From the results of the hydrological modelling of both fieldwork areas in the Gelderse Vallei basin it can be concluded that the relationships between local and external water management and geohydrological conditions in the area are crucial in maintaining or restoring upward seepage. Both areas are too small for upward seepage and the accompanying high groundwater levels to be restored (Van der Schaaf 1998). Large-scale conservation of precipitation water, as done in the Korenburgerveen area, may achieve in the required high ground water levels year-round, but in the long term will stimulate acidification of fen meadows.

The second question (B) concerned the effect of restoration measures on the factors that control the base regulation and nutrient availability in the soil. In the Bennekomse Meent, I expect that the gradual acidification will be reversible due to the current high base status of the soil. In the *Cirsio-Molinietum* sites the base saturation exceeded 80% of the cation exchange capacity (CEC), Buil 1999 and Alterra 1999, which is safely above the critical level of 25%, below which sites are considered severely and permanently acidified (Kemmers et al. 2003). The ANC was correspondingly high (Figure 1). If high groundwater levels in summer are restored in the Bennekomse Meent, especially in the lower plots, soil acidity will be buffered by ionic exchange with soil adsorption complex in the long term. The presence of iron oxides in soil guarantees the required capacity of the system to generate internal alkalinity upon reduction. To restore the base status of the acidified high plots it will be necessary to increase the external supply of alkalinity. In certain other restoration projects, acidification was successfully reversed after raising the groundwater levels and increasing the calcium supply by removing the acidified topsoil (e.g. in De Barten, cf. Grootjans et al. 2002). Therefore, I conclude that removal of the acidified topsoil, combined with superficial drainage to discharge rainwater, is advisable in the Bennekomse Meent, especially in lower plots where base-rich groundwater still occurs in the root zone (Chapter 5; Buil 1999; Terlouw 2003).

The restoration of high groundwater levels in the winter appeared to be effective to reverse the internal eutrophication in *Cirsio-Molinietum* sites of the Bennekomse Meent, even though summer groundwater levels were low. Chapter 2 reported that the effects of several consecutive dry summers on plant species composition disappeared within ten years. This recovery is due to the increased groundwater levels, the buffered nutrient cycling (Chapter 4) and the removal of nutrients by haymaking. The resilience after eutrophication in the Bennekomse Meent fen meadow is also shown by the fertilisation experiment (Chapter 3), as the increase in biomass production after N fertilisation had already disappeared after a year and by the fourth year the effect of P fertilisation on species composition had almost faded away. Even in fen meadows where fertilisation has caused large changes in species composition and aboveground biomass, mowing without fertilisation could reverse these changes, provided that there is upward seepage of base-rich groundwater. In the Drentse Aa brook valley reserve, which had been intensively fertilised for 10-30 years, it took up to 20 years to restore the target species, depending on the amount of nutrients accumulated during fertilisation (Bakker & Olff 1995).

Considering the Korenburgerveen area with its strongly declined external alkalinisation, I infer that the success of turf stripping in increasing the acid buffer capacity depends greatly on internal alkalinisation and might be temporary. Given the increasing soil pH but no increased calcium saturation of the CEC reported in Chapter 5, it can be concluded that soil acidity has been weakly buffered by dissolved bicarbonate, supplied by reduction in stripped plots in this fen meadow. In addition, in the stripped plots I found a sufficient redox capacity and anaerobic soil conditions, which are favourable for internal alkalinisation. The anaerobic conditions are due to the permanently high groundwater levels brought about by water conservation within a large area. When infiltration intensity and acidification increase in fen meadows like the Korenburgerveen, which is suggested by the succession, superficial organic horizons of dead roots (box 2) will develop in wet sites. In such sites, stripping will not restore a high soil base status. Although stripping will expose soil horizons that are not yet weathered, in due time the new topsoil will be depleted of iron, leached and acidified. As yet, there are no such sites in the fen meadows of the Korenburgerveen investigated in this research, but they have developed in several other Dutch nature reserves where restoration has failed (Kemmers et al. 2003).

In the former agricultural fields of the Veenkampen, acid buffering decreased only slightly, despite the infiltration of precipitation water. Due to the high buffer capacity of the clayey soil and former fertilisation, the pH remained at about 5.5. Contrary to expectations, even subterranean irrigation with deep groundwater did not increase soil pH. The higher water table in the irrigated part did reduce nitrogen mineralisation (by c. 20% according to Berendse et al. 1994 and by 70% according to Oomes et al. 1997). It also decreased plant-available phosphate in the course of ten years (Chapter 6). However, the dry matter production and the uptake of N and P did not decrease after rewetting and, four years after the sod cutting, the dry matter production on the stripped plots was not different from the control plots (Oomes et al. 1996, 1998). This is attributable to the relatively high N and P content of the soil, the limitation of dry matter production by K (Oomes 1995; Kapfer 1994; Olff & Pegtel 1994) and the dominance of plant species that are adapted to anaerobic soil conditions.

The negative effect of rewetting on the N mineralisation and P availability in the Veenkampen experiment and the absence of an effect on decomposition (Berendse et al. 1994) are contradictory to the results of the rewetting experiment of Van Dijk et al. (2004). A possible reason for the disparity might be the difference in the original soil pH. In the experiment of Van Dijk the pH increased from 3.5 to about 7 in response to infiltration of calcareous seepage water (Van Dijk et al. 2004); this might have resulted in an increased mineralisation and solubility of P compounds (P-FeOOH and P-$CaCO_3$, Chapter 4). By contrast, the soil pH of c. 5.5 in the Veenkampen hardly changed after rewetting (Chapter 6; Oomes et al. 1996) and did not enhance the nutrient availability.

I conclude that in nature reserves, when groundwater levels increase, the presence of calcium in the root zone may result in a recharge of the CEC and a subsequent increased ANC. When base cations have disappeared, restoring high groundwater levels may at best achieve slight acid buffering due to internal alkalinisation. In addition to restored high groundwater levels, haymaking is an important means of maintaining and restoring nutrient-poor conditions. When exfiltration of groundwater has declined, stripping in combination with a superficial discharge of rainwater may restore the soil conditions necessary for species-rich fen meadows in the longer term. Both measures are a prerequisite for some restoration success when exfiltration is weak. In former agricultural fields on peaty soils, rewetting and sod cutting will not result in the recovery of nutrient-poor conditions.

The third question (C) concerned the extent to which we may be able to restore the target plant communities. In the Bennekomse Meent all the characteristic fen meadow plant communities persisted, despite low groundwater levels in summer. The fact that the gradient of plant communities is declining (Chapter 2) suggests that this persistence is possible because of the spatial heterogeneity and the buffering that is slowing down changes in the soil. The succession towards *Junco-Molinion* plant communities might have been facilitated by efficient seed dispersal from neighbouring sites. I expect that when the resilience of the system decreases further in response to low groundwater levels in summer, *Calthion* species will disappear and plant diversity will decline. In such cases, sod cutting can be harmful for endangered species (Jansen et al 2004), as it can lead to the depletion of persistent seed banks (Grootjans et al. 2002). On the other hand, an increase in the upward seepage of base-rich groundwater is likely to result in maintenance of the *Calthion* species. In the low sites, stagnation of rainwater resulted in succession towards *Parvocaricetea* plant communities (Chapters 2, 5; Van Diggelen et al. 1991). Since base-rich groundwater is present in the subsoil, promoting superficial discharge of precipitation water by digging shallow ditches may retard this succession. It might be possible to reverse the succession from *Parvocaricetea* towards *Junco-Molinion* plant communities in such sites if no drastic shift occurs towards a growing moss carpet (box 2).

In the Korenburgerveen fieldwork area, the increased buffering of acidity after stripping (Figure 1) resulted in the recovery of some *Junco-Molinion* species, including several Red List species. However, the succession towards a complete *Junco-Molinion* community did not continue, despite high groundwater levels. I expect that the observed succession towards small sedges in response to conservation of precipitation represents a transition towards the acidophilous plant communities that dominate in the control plots. The restoration of all original fen meadow species is not an option, even though upward seepage would be restored in a short time, since there may not be seeds of these species in the seed bank and the species have disappeared in the surroundings since the 1950s (Westhoff & Van Dijk 1952).

In eutrophied and intensively drained agricultural fields, resuming the traditional management of haymaking will not lead to the recovery of original plant communities, because the soil has changed irreversibly. Although in the Veenkampen experiment 17 years of haymaking without fertilisation decreased the dry matter yield to the level of the original litter meadow, hardly any new plant species established. Oomes et al. (1998) concluded that haymaking alone was insufficient to reduce the availability of N and P in soil to the required low levels. They further found that combining sod cutting to a depth of 5 or 10 cm with haymaking reduced the uptake of N and P in the Veenkampen experiment, but the uptake remained far greater than that commonly found in *Cirsio-Molinietum* communities. The combination of sod cutting with rewetting and haymaking was more successful, since it created a favourable vegetation structure for the establishment of new (Red List) species. As the dispersal mechanisms of these species have been shown to be ineffective, the seeds must have survived in the seed bank for up to 50 years (Van Dorp 1996). However, it can be questioned whether these target species will persist, since aboveground biomass is gradually increasing and acidification is proceeding. I conclude therefore that in degraded peat soils of former agricultural land, in spite of sod cutting and rewetting it is impossible to restore the conditions that are required for the recovery of the original plant communities.

The final conclusion of this study is that the success of fen meadow restoration depends greatly on the feasibility of restoring wet, mesotrophic and base-rich conditions by increasing the upward seepage of groundwater within the framework of the regional hydrological system. If the soil mechanisms that buffer the required conditions cannot be restored by hydrological measures or additional measures such as turf stripping, fen meadow restoration will only produce fragmentary plant communities that deviate considerably from the reference communities. Therefore, when defining targets for restoration in fen meadows, one must take into account that often more acid conditions than the original ones will develop. Consequently, one has to investigate alternative target communities that are characteristic of relatively acid and dry or wet conditions (Van der Hoek & Van der Schaaf 1988).

Given this wide choice of alternative targets, the nature management of fen meadows needs to be strategically planned on the basis of the ecohydrological concept and concepts about the dynamics in soil and vegetation. It is especially important to use a cyclic planning process, since defining the targets of ecological restoration should be strongly interlinked with monitoring of the results of the restoration (Dierssen 1994; Bakker et al. 2001; Van Langevelde et al. 1994). I conclude that restoration projects at a local scale should be regularly monitored, in order to evaluate whether targets will be met within a reasonable time span.

The current management plans for the fen meadows on my fieldwork sites are based on the results of over twelve years of monitoring and demonstrate the practical value of cyclic planning. In this type of approach, the planning of restoration measures is based on the sustainability of the required environmental conditions. This is preferable to making plans where success is judged in terms of target species, as these species may well prove transient.

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Summary

Until 50 years ago, fen meadows were common in The Netherlands. Fen meadows are wetland plant communities on peaty soils, derived by draining and exploiting fens for haymaking. This study focuses on poorly productive mesotrophic *Junco-Molinion* communities (the *Cirsio dissecti-Molinietum* association in particular), including gradients to more acidophilous *Parvocaricetae* and more productive, eutrophic *Calthion* plant communities. The communities investigated occur in brook valleys that are influenced by regional hydrology. High groundwater levels and upward seepage of base-rich ground water are prerequisites for the wet, neutral to alkaline and nutrient-poor conditions that these communities require. On top of that, the more eutrophic fen meadows are influenced by inundation with surface water.

Almost everywhere in the Netherlands these fen meadows have become more eutrophied and acidified. Consequently, biomass production has increased and many species characteristic of base-rich and nutrient-poor conditions have become locally endangered or extinct. A major cause of the eutrophication and acidification has been the lowering of groundwater levels by exploitation of deep groundwater and drainage for agriculture. Since the 1980s there have been many attempts to restore disturbed fen meadows, focusing on restoring the original hydrological processes and soil conditions. In some cases the restoration has succeeded with relatively little effort, while in other cases the success has been only temporary or has failed. The uncertainty of the results of restoration attempts is due to lack of knowledge of the hydrological and biogeochemical processes that drive the changes in plant communities. Monitoring has indicated that irreversibility and hysteresis play key roles in restoration success.

The aim of this study was to investigate the mechanisms that determine the effectiveness of measures aimed at restoring species-rich fen meadow communities. The general hypothesis was that recovery of the original species-rich fen meadow communities requires the processes responsible for buffering the neutral soil pH and the low availability of nutrients to be restored. The study examines the control of nutrient availability and soil acidity by groundwater level and chemistry and focuses on the consequences of upward seepage of base-rich groundwater. In addition, the response of plant communities to changes in hydrological conditions was investigated, paying special attention to the persistence of re-established species. The fieldwork was done in two nature reserves, the Bennekomse Meent and the Korenburgerveen, and in an experimental field (the Veenkampen), which is a former fen meadow that was intensively used for agriculture.

Preliminary research into the geohydrological and ecohydrological conditions of the Bennekomse Meent area had shown that this fen's resilience to influences from the intensively used surroundings was decreasing. The upward seepage of base-rich groundwater had weakened, so the water table had fallen and the soil was being gradually acidified by infiltrating rainwater. The lower water table also resulted in a temporary, internal eutrophication after consecutive drier years.

We hypothesised in Chapter 2 that falling groundwater levels may not lead to a boosted aboveground biomass production in *Cirsio-Molinietum* fen meadows, if nutrient limitation persists. Instead, depending on drainage intensity and microtopography, acidification may trigger a shift to drier and more nutrient-poor plant communities. In a long-term study

along a gradient in drainage intensity we analysed shifts in a *Cirsio-Molinietum* in relation to the driving soil processes at different scales. In addition, we evaluated the efficacy of various local hydrological measures for restoration (Chapter 2). It appeared that aboveground biomass increased only slightly, despite lower summer groundwater. This was due to a limited availability of nutrients: K in the well-drained plots, P in the intermediate plots and N in the plots without drainage, plus removal of hay. On the dry sites we found an increase of acidophilous *Junco-Molinion* species. On the wet sites, *Caricion curto-nigrae* species increased. Both changes were attributed to soil acidification occurring when rainwater becomes more influential than base-rich groundwater. The extent of the shift in species composition depends primarily on the drainage intensity and secondarily on microtopography. We conclude that this succession happened at the cost of *Calthion* species, except lower in the gradient of drained sites, where this change was counteracted by the presence of buffered groundwater. Water conservation resulted in the recovery of high groundwater levels in spring but not in summer. Local hydrological measures in the surroundings of the reserve largely failed to restore wetter and more basic conditions. One option for the sustainable conservation of the typical plant communities of the *Cirsio-Molinietum* to *Calthion* gradient might be the reintroduction of occasional inundation with buffered surface water.

Since nutrient-poor surface water is rarely available in the Bennekomse Meent, we investigated the consequences of incidental inundation with nutrient-rich surface water (Chapter 3). Nutrient pulses may change the aboveground biomass and the plant species composition of species-rich fen ecosystems for years. To investigate the persistence of these changes we conducted a single pulse fertilisation experiment with N and P in two *Cirsio-Molinietum* sites that differed in drainage intensity. We monitored biomass production and species composition during four years. In the undrained site, N fertilisation boosted total biomass production, but only in the first year. No N-induced shift was observed in species composition. P fertilisation brought about an increase in biomass and a change in species composition from a community dominated by *Carex panicea* to a community with abundant *Holcus lanatus*, but not before the second year. In the drained site, N fertilisation had no effect. P fertilisation resulted in a shift in species composition similar to that observed at the undrained site, while biomass did not increase. At both sites the P-induced shift in species composition declined gradually during the four-year observation period. We infer that the decrease of the stress-tolerant *C. panicea* might be a consequence of the increase of more competitive species such as *H. lanatus*. The fast decline of the N effect on biomass production after the first year is probably due to increased denitrification and removal of biomass for haymaking. The delay in the P-effect on biomass and species composition and the persistence of the P-effect on species composition are ascribed to fast immobilisation and subsequent slow release of fertiliser P in the peat soil. The gradual decline in the P-effect on biomass is ascribed to biomass removal. The results of the fertilisation experiment show that the fen meadow can recover from incidental flooding with nutrient-rich water, but increasing the flooding frequency beyond once in five years will cause a permanent shift in species composition.

Low availability of nitrogen and phosphorus appears to be a prerequisite for the conservation of species-rich fen-meadows ecosystems (Chapters 2 and 3). Chapter 4 gives an overview of the cycling of P in *Cirsio-Molinietum* sites. The species composition of these communities seemed to be determined by the inorganic P concentration in the soil solution, which is known to depend on soil water pH. Biomass production is controlled by the annual P flux that results from turnover of the large pool of organic P, which depends on the groundwater level. Therefore, the prerequisites for maintaining a low inorganic P concentration in the soil solution are continuous upward seepage of calcareous groundwater into the root zone, and the consequent acid buffering and high groundwater levels. We used hydrological models to predict the effect of restoration measures on the quantity and quality of water in the root zone. The model calculations indicated that the deteriorated site conditions might be improved to favour a *Cirsio-Molinietum* fen meadow by limiting the deep drainage, which could be done by partially filling ditches in the surroundings of the reserve. The calculations indicated that the effectiveness of less deep drainage might be increased by taking measures inside the reserve, such as removal of surplus rainwater and turf stripping to remove acidified topsoil and lower the surface level.

The prediction that turf stripping and rainwater discharge are effective measures for restoring the nutrient-poor, buffered conditions required by species-rich fen meadow communities was investigated in an acidified fen meadow in the Korenburgerveen reserve (Chapter 5). After stripping the degraded *Cirsio-Molinietum* vegetation and the acidophilous moss carpet we monitored the changes in vegetation, soil, groundwater level and groundwater chemistry during twelve years. After the first five years, many species from the target communities had returned in the stripped plots. However, further succession proceeded towards more acidophilous plant communities, indicating a decreasing acid buffer capacity of the soil. Turf stripping had exposed a nutrient-poor soil layer with a greater acid-buffering capacity, but the increase in buffer capacity was only temporary, since calcium concentrations in the groundwater declined during the twelve years due to the weakening of upward seepage. Nonetheless, the soil pH of the stripped plots increased significantly over time, though it did not reach the level found in the target community site. Since sulphate concentrations in the groundwater decreased significantly, whereas the bicarbonate concentration increased, we inferred that in the stripped plots there was internal alkalinisation driven by sulphate reduction. In addition, we found that during prolonged wet periods excess precipitation was discharged from the stripped plots as surface runoff. Our conclusion was that the internal alkalinisation and the runoff of excess precipitation could initially compensate for the decrease in external alkalinisation and neutralise the proton production. However, these positive effects of turf stripping might fade away, since surface runoff and redox capacity will decrease in the long term.

To gain insight into the effectiveness of restoration measures in severely altered soils, we investigated the effect of rewetting measures on key processes in the soil of a previously intensively drained and fertilised former fen meadow in the Veenkampen experimental field (Chapter 6). In this experiment it was intended to regenerate wet nutrient-poor soil conditions by conserving rainwater and by subterranean irrigation with deep groundwater, in combination with haymaking. Conservation of precipitation appeared to be an inadequate measure to restore high groundwater levels and nutrient-poor conditions in the clayey topsoil. Monitoring showed that subterranean irrigation resulted in higher groundwater levels throughout the year, but the increased infiltration of rainwater stimulated acidification of the topsoil. Higher groundwater levels reduced the decomposition of organic matter and the mineralisation of nitrogen and increased organic matter content. Fertilisation had resulted in a major accumulation of inorganic P. A striking effect of rewetting by subterranean irrigation was the decrease of plant-available phosphate during the ten years of this experiment. This decrease might be the result of the dissolution of iron phosphate complexes under the anaerobic conditions and the subsequent leaching of P to the subsoil. The slow decrease in the inorganic P showed that hydrological measures were not sufficient to reverse eutrophication of this peat soil. Laboratory experiments with Veenkampen soil showed that even subterranean irrigation with deep groundwater could not seriously reverse eutrophication, by increasing P fixation, due to the low calcium content of this groundwater.

In order to judge the success of restoration measures in the long term, we evaluated the recovery of the mechanisms that determine the resilience of fen meadow ecosystems, i.e. acid buffering and strong nutrient limitation (general discussion in Chapter 7). The persistence of re-established species was also evaluated. The benchmark situation was an original, undisturbed fen meadow ecosystem. The fen meadow sites we studied are in exfiltration areas belonging to large groundwater systems. Consequently, available nutrient and proton concentrations in the soil are buffered at a low level by a stable flux of groundwater with a constant chemical composition. Nutrient availability is kept low by the export of nutrients by haymaking, and acidification can occur only superficially because drainage is limited. In addition, the resilience of these fen meadows to external influences is supported by an important positive feedback in the nutrient cycle: between the effects of nutrient availability on the species composition and the effects of dominant species on soil nutrient mineralisation. Provided that these resilience mechanisms are not overloaded or disturbed, stable soil conditions may persist for a very long time, facilitating the development of a species-rich fen meadow vegetation.

Having described the reference situation, we focus on the response of fen meadows to changes in hydrology. We found a gradual response in the Bennekomse Meent and sudden responses in the other fieldwork areas, reflecting the extent to which exfiltration had decreased. In the Korenburgerveen there was a drastic shift to acidified and species-poor plant communities dominated by acidophilous mosses. The growing moss carpet resulted in an irreversible acidified soil. A severely irreversible eutrophication of the soil occurred in the drained and fertilised Veenkampen field.

Finally, the effect of some restoration measures on hydrology, soil conditions and vegetation is evaluated in Chapter 7. If there is sufficient discharge of groundwater from deep aquifers, local and external water management may be successful in restoring the upward seepage of base-rich groundwater into the root zone. However, two of our study areas (Bennekomse Meent and Veenkampen) were too small for upward seepage to be increased by filling in ditches in the surroundings. Hence, they suffer from infiltration of precipitation and low groundwater levels in summer. Conservation of precipitation in these small reserves stimulates acidification of the topsoil. When exfiltration has disappeared (e.g in the Veenkampen), irrigation with deep groundwater may be used to maintain a high groundwater level in the summer, but the acidification of the topsoil will continue due to the downward movement of the irrigated water. Large-scale water conservation in the Korenburgerveen area did achieve high groundwater levels throughout the year, but will result in acidified fen meadows in the long term.

The opportunities for the recovery of the crucial buffer mechanisms in the soil are related to upward seepage intensity, which decreased in the sequence: Bennekomse Meent, Korenburgerveen and Veenkampen. The gradual acidification in *Cirsio-Molinietum* sites in the Bennekomse Meent might be reversible if summer groundwater levels rise, due to the high base status and the redox capacity of the soil and influence of upward seepage. Incidental flooding with eutrophic, base-rich surface water to reverse acidification is an option, since the effects of eutrophication on biomass production and species composition will fade away within about five years. Turf stripping, combined with discharge of excess precipitation, will enable hysteresis to be avoided when the soil base status of superficially acidified soils is recovering (Bennekomse Meent). It is essential to slow down acidification when exfiltration has disappeared and topsoil had irreversible acidified (Korenburgerveen, Chapter 5). In addition to hydrological measures and turf stripping, haymaking is the tool to maintain nutrient-poor soil conditions in nature reserves. These restoration measures are not effective in formerly intensively used fields in fen areas, in the short term, since soil conditions have been changed irreversibly to a great depth.

The proposed measures may retard or reverse the succession from *Junco-Molinion* communities towards acidophilous dry or wet plant communities in sites where there is upward seepage into the root zone. On the other hand, in wet sites where exfiltration has disappeared, succession towards *Parvocaricetea* plant communities will occur, in spite of turf stripping and an initial reappearance of *Junco-Molinion* target species. Although rewetting and sod cutting has resulted in target species returning to formerly farmed fields in fen areas, these species will not persist, since biomass production is gradually increasing and there is ongoing acidification.

The findings of this research on the dynamics of fen meadows emphasize the need for a cyclic planning process in fen meadow management. First, feasible plant communities and restoration measures should be selected, based on sustainable hydrological conditions and the reported effectiveness of restoration measures. Secondly, a regular inspection of the key-processes described in this study is essential to monitor the actual effectiveness of the measures applied, so that adjustments can be made when needed. This cyclic approach is preferable to basing plans simply on the temporary recovery of target species.

Samenvatting

Tot 50 jaar geleden kwamen soortenrijke natte schraalgraslanden nog algemeen voor in Nederland. Dit onderzoek is in het bijzonder gericht op laagproductieve hooilanden, zogenaamde blauwgraslanden (*Junco-Molinion*, in het bijzonder de associatie *Cirsio dissecti-Molinietum*), die veelal zijn ontstaan uit moerassen door drainage en een jarenlang beheer van maaien en afvoeren. Blauwgraslanden zijn gebonden aan bodems met een neutraal-basisch karakter en een lage nutrientenbeschikbaarheid. Deze bodemeigenschappen zijn het gevolg van kwel van basenrijk grondwater en hoge grondwaterstanden. Bij dit onderzoek is veel aandacht besteed aan de overgangen in blauwgraslanden naar meer zure Kleine zeggen gemeenschappen (*Parvocaricetae*) en meer voedselrijke Dotterbloemhooilanden (*Calthion*). Al de onderzochte vegetaties zijn gelegen in beekdalen die onder invloed staan van regionale grondwatersystemen.

Door verdroging zijn de soortenrijke natte schraalgraslanden in Nederland bijna overal voedselrijker geworden en/of verzuurd. Daardoor is in veel gevallen de bovengrondse biomassa toegenomen en zijn veel kenmerkende soorten in hun voorkomen bedreigd geraakt of verdwenen. Een belangrijke oorzaak van deze verdroging is de grondwaterstandsdaling, als gevolg van de winning van diep grondwater en versterkte drainage ten behoeve van de landbouw. Pogingen tot het herstel van verdroogde schraalgraslanden, waarbij men zich richtte op het herstel van de hydrologie en de bodem, gingen gepaard met wisselend succes. Soms trad er al na kleine ingrepen herstel op terwijl in andere gevallen het herstel, ondanks grote inspanningen, mislukte. Succes bleek vaak tijdelijk te zijn. Deze wisselende resultaten bij herstelprojecten hangen samen met het beperkte inzicht dat er is in de hydrologische en biogeochemische processen die bepalend zijn voor vegetatieveranderingen. Uit de monitoring van hydrologie, bodem en vegetatie bij herstelprojecten bleek, dat hysteresis en irreversibiliteit een sleutelrol zouden kunnen spelen bij het succes van herstelmaatregelen.

In dit proefschrift worden de mechanismen geanalyseerd die de effectiviteit bepalen van enkele hydrologische maatregelen en plaggen, op het herstel van soortenrijke, natte schraalgraslanden (in het bijzonder blauwgrasland). De algemene hypothese van mijn onderzoek is dat voor dit herstel de reconstructie vereist is van de processen die zorgen voor de buffering van een neutrale pH en voor een lage nutrientenbeschikbaarheid in de bodem. Het onderzoek richt zich specifiek op de regulerende werking van kwel op de zuurhuishouding en op de nutrientenbeschikbaarheid in de bodem, via het peil en de chemische samenstelling van het grondwater. Daarbij aansluitend, heb ik onderzoek gedaan naar de respons van plantengemeenschappen op de veranderingen in hydrologie en bodem die door herstelmaatregelen waren gerealiseerd. Het veldonderzoek heb ik gedaan in twee natuurreservaten: de Bennekomse Meent en het Korenburgerveen, en in een proefaccomodatie (de Veenkampen). In de proefaccomodatie is de regeneratie van natte, schraalgraslanden onderzocht in een gebied, dat intensief door agrariërs was gebruikt. Voorafgaand aan het onderzoek heb ik met anderen oriënterend (eco) hydrologisch onderzoek uitgevoerd in het zuidelijk deel van de Gelderse Vallei, waarin de Bennekomse Meent en de Veenkampen zijn gelegen. Dit onderzoek toonde aan dat door de afname van de kwel de kwetsbaarheid van het blauwgrasland in de Bennekomse Meent voor verdroging was toegenomen.

In hoofdstuk 2 wordt verondersteld dat grondwaterstandsdaling in een blauwgrasland niet tot een sterke toename van de bovengrondse biomassaproductie leidt indien de groei door de geringe beschikbaarheid van nutrienten wordt beperkt. Grondwaterstandsdaling kan dan gepaard gaan met verzuring en een successie naar drogere en meer voedselarme plantengemeenschappen, in een mate die afhankelijk is van de drainage intensiteit en het relief. Op enkele locaties in het blauwgrasland van de Bennekomse Meent, die verschillen in drainage intensiteit, onderzochten we per hoogtezone de veranderingen die in de soortensamenstelling gedurende tien jaar zijn opgetreden, in relatie tot grondwaterstanden en bodemprocessen. Op basis van de verkregen resultaten, werd tevens de effectiviteit van enkele locale hydrologische herstelmaatregelen geevalueerd. De toename van de bovengrondse biomassaproductie bleek in deze periode gering te zijn, ondanks de lagere zomer grondwaterstanden. Dit hangt enerzijds samen met de beperkte beschikbaarheid van nutrienten: K, P en N, respectievelijk op de sterk, matig en niet gedraineerde locaties. Anderzijds heeft het hooien, door de afvoer van mineralen, gezorgd voor een voortdurende verschraling. Op de droge plaatsen vond een toename plaats van *Cirsio-Molinietum nardetosum* soorten. Op de natte plaatsen nam het aantal *Caricion curto-nigrae* soorten toe. Beide veranderingen zijn het gevolg van verzuring van de bodem die optreedt wanneer de invloed neerslagwater ten opzichte van die van basenrijk grondwater toeneemt. De mate van de soortsverandering bleek allereerst af te hangen van de drainage intensiteit en vervolgens van het relief. Wij concluderen dat deze successie ten koste gaat van het aantal *Calthion* soorten. Op de laagste plaatsen van gedraineerde locaties wordt deze successie door de aanwezigheid van gebufferd grondwater geremd. Waterconsering resulteerde in het herstel van hogere grondwaterstanden in het voorjaar, maar niet in de zomer. Hydrologische maatregelen ter vernatting van de omgeving, leiden niet tot nattere en minder zure condities in het reservaat. Aanbevolen wordt om incidentele inundaties met gebufferd oppervlaktewater weer toe te laten, tot behoud van de kenmerkende *Cirsio-Molinietum* / *Calthion* gradiënten in het blauwgrasland.

Omdat meestal alleen voedselrijk oppervlatewater voor inundatie beschikbaar is, werd er vervolgens onderzoek gedaan naar de effecten van een incidentele nutrientengift op blauwgrasland (Hoofdstuk 3). Incidentele belasting met nutrienten zou de bovengrondse biomassproductie en de soortensamenstelling van blauwgrasland jarenlang kunnen beinvloeden. In een bemestingsexperiment met stikstof en fosfor volgden we gedurende vier jaar de veranderingen in bovengrondse biomassproductie en soortensamenstelling op twee locaties die verschillen in drainage intensiteit. De bemesting werd alleen in het eerste jaar uitgevoerd. Op de niet gedraineerde locatie, leidde de N bemesting tot een sterke toename van de bovengrondse biomassaproductie, maar alleen in het eerste jaar. Er werd geen N-effekt op de soortensamenstelling aangetroffen. P bemesting had ook een toename van de biomassa tot gevolg maar dit gebeurde alleen in het tweede jaar. Bovendien veroorzaakte P bemesting een verschuiving in de soortensamenstelling: van een plantengemeenschap gedomineerd door *Carex panicea* naar een plantengemeenschap met een dominantie van *Holcus lanatus*. Op de gedraineerde locatie had N bemesting geen effecten. P bemesting resulteerde daar in dezelfde verschuiving in de soortensamenstelling als op de niet gedraineerde locatie, hoewel de biomassa niet toenam. Op beide locaties nam het effect van de P bemesting op de soortensamenstelling gedurende de waarnemingsperiode langzamerhand af. Wij menen dat de afname van de stress-tolerante soort *C. panicea* het gevolg kan zijn van de toename van de meer concurrentiekrachtige soort *H. lanatus*. De snelle afname van het N-effect op de biomassaproductie, na het eerste jaar, is waarschijnlijk het gevolg van een toegenomen denitrificatie en van het afvoeren van biomassa door het hooien. Het vertraagde P-effect op de biomassa en de soortensamenstelling en de lange nawerking van het P-effect op de soortensamenstelling kunnen worden toegeschreven aan de snelle immobilisatie gevolgd door een langzame mobilisatie van gegeven P in de venige bodem. De geleidelijke afname van het P-effect op de biomassa kan worden verklaard door het hooien. De resultaten van het bemestingsexperiment laten zien dat een blauwgrasland zich na een incidentele overstroming met voedslerijk oppervlaktewater kan herstellen. Wanneer de overstroming echter vaker dan eens per vijf jaar optreedt, zal de soortensamenstelling blijvend veranderen.

Volgens hoofdstuk 2 en 3 is de lage beschikbaarheid van stikstof en fosfor een eerste vereiste voor het behoud van soortenrijke blauwgraslanden. De biogeochemische processen die hierbij regulerend optreden worden in hoofdstuk 4 beschreven. In dit hoofdstuk wordt het correlatieve verband tussen de grondwaterstand en de nitrificatie getoond en er wordt een overzicht gegeven van de P-kringloop in een blauwgrasland (Bennekomse Meent). De soortensamenstelling van het blauwgrasland lijkt te worden bepaald door de concentratie van anorganisch P in de bodemoplossing, die afhankelijk is van de pH van het bodemwater. De biomassaproductie wordt gereguleerd door de jaarlijkse P stroom die afkomstig is uit de mineralisatie van organisch P. In de bodem is een grote hoeveelheid organisch P aanwezig. De mineralisatie (van N en P) wordt geremd door de, overheersend hoge, grondwaterstanden. Wij concluderen dat het voorkomen van basenrijke kwel, door de daaraan verbonden zuurbuffering en hoge grondwaterstanden, een essentiële voorwaarde is voor het behoud van een lage P concentratie in de bodemoplossing. Door middel van enkele hydrologische modellen zijn voorspellingen gedaan over de effecten van herstelmaatregelen op het peil en de chemische samenstelling van het water in de wortelzone van het blauwgrasland. Deze voorspellingen geven aan dat het verminderen van diepe drainage in de omgeving van het reservaat, hetgeen gerealiseerd kan worden door het dempen of verondiepen van sloten, zal leiden tot verbetering van de standplaatscondities van het blauwgrasland in het reservaat. De effectiviteit van deze externe maatregelen kan worden vergroot door aanvullende maatregelen binnen het reservaat te nemen, zoals het aanbrengen van ondiepe greppels om het neerslagoverschot af te voeren of plaggen om het maaiveld te verlagen.

De voorspelling dat de afvoer van het neerslagoverschot in combinatie met plaggen, effectief kan zijn voor het herstel van voedselarme, gebufferde omstandigheden die vereist zijn voor soortenrijke blauwgraslanden, werd nader onderzocht in een verzuurd blauwgrasland van het Korenburgerveen reservaat (Hoofdstuk 5). Nadat de uitgangssituatie was geanalyseerd werd hier in een veldexperiment de gedegradeerde vegetatie, inclusief een verzuurde 15 cm dikke moslaag, verwijderd. We hebben vervolgens, gedurende twaalf jaar, de veranderingen gemeten in vegetatie, bodem, en grondwater (peil en chemische samenstelling). Binnen de eerste vijf jaar werden er op de plagplekken weer kenmerkende blauwgraslandsoorten aangetroffen. Nadien echter nam het aandeel van zuurminnende soorten toe, wat wijst op een afname van het zuurbufferend vermogen van de bodem. Door plaggen was er een voedselarme bodem met een hoog zuurbufferend vermogen gecreeerd, maar dit bleek tijdelijk te zijn als gevolg van de afname van de calciumconcentratie van het grondwater en de vermindering van de kwel. Desondanks bleek de pH van de bodem op de geplagde plekken in de tijd significant toe te nemen, hoewel de waarden lager bleven dan de pH in de bodem van een nabijgelegen niet verzuurd blauwgrasland. Wij menen dat deze pH toename op plagplekken het gevolg is van interne alkalinisatie door sulfaatreductie, omdat er tevens een significante toename van het bicarbonaaat en een significante afname van het sulfaatgehalte van het grondwater werd aangetroffen. Wij vonden bovendien dat op plagplekken bij langdurige natte perioden het neerslagoverschot over het bodemoppervlak kan afstromen. Wij concluderen daarom dat als gevolg van het plaggen verzuring kan worden tegengegaan ondanks een afnemende kwel van basenrijk grondwater. Deze positieve effecten van plaggen zullen echter op den duur verdwijnen, door een afname van de redox capaciteit van de bodem en door een vermindering van de oppervlakkige afvoer tijdens de successie.

Om inzicht te verkrijgen in de effectiviteit van herstelmaatregelen in bodems die sterk zijn beinvloed, onderzochten we het effect van vernatting op de belangrijkste bodemprocessen in een gebied met een voormalig agrarisch gebruik (Hoofdstuk 6). Het onderzoek vond plaats in de proefaccomodatie De Veenkampen, waar soortenrijke natte schraalgraslanden zijn verdwenen door intensieve drainage en bemesting. In het vernattingsexperiment is onderzocht, bij een hooilandbeheer, in hoeverre de oorspronkelijke eigenschappen van de bodem kunnen worden hersteld door het conserveren van neerslagwater en door het infiltreren van de bodem met diep grondwater. Uit de monitoring bleek dat de vereiste hoge grondwaterstanden en de voedselarme condities in de bodem niet bereikt kunnen worden met het conserveren van neerslagwater. Het infiltreren van diep grondwater resulteert weliswaar in hogere grondwaterstanden, maar dit gaat gepaard met een sterkere wegzijging van neerslagwater waardoor de bodem verzuurt. Door de gerealiseerde hogere grondwaterstanden wordt de decompositie van de organische stof en de stikstofmineralisatie gereduceerd, hetgeen leidt tot een toename van het organischstofgehalte. De voormalige bemesting heeft de voorraad anorganisch P in de bodem sterk verhoogd. Opvallend is dat als gevolg van het infiltreren gedurende tien jaar de hoeveelheid voor planten beschikbaar fosfaat in de bodem is afgenomen. Deze afname wordt waarschijnlijk veroorzaakt doordat, onder de anaerobe omstandigheden, ijzerfosfaatcomplexen in oplossing gaan en vervolgens uitspoelen naar de ondergrond. De langzame afname van anorganisch P laat zien dat hydrologische maatregelen niet effectief zijn om de opgetreden eutrofiering van deze kleiige veengrond op korte termijn terug te draaien. Aanvullende experimenten die wij in het laboratorium uitvoerden met bodemmonsters uit de Veenkampen toonden aan dat het geinfiltreerde water door het lage calciumgehalte niet geschikt is om een toename van de P fixatie te bereiken.

Om het succes van de bestudeerde herstelmaatregelen op de lange termijn te kunnen beoordelen, evalueer ik hoofdstuk 7 in hoeverre door deze maatregelen de veerkracht van natte schraalgraslanden (blauwgraslanden) hersteld kan worden. Deze evaluatie is gericht op de mechanismen die in de bodem het zuurbufferend vermogen en de beperkte beschikbaarheid van nutrienten reguleren en op de duurzaamheid van de plantensoorten die zich opnieuw vestigden.

Allereerst wordt in dit hoofdstuk een algemene ecohydrologische beschrijving gegeven van de oorspronkelijke blauwgraslanden uit de onderzoeksgebieden. Al de bestudeerde (voormalige) blauwgraslanden zijn gelegen in kwelgebieden die gevoed worden met regionaal grondwater. Door de continue toestroming van grondwater, waarvan de chemisch samenstelling nauwelijks fluctueert, wordt in deze kwelgebieden de beschikbaarheid van nutrienten en de concentratie van protonen op een laag niveau gebufferd. Bovendien wordt de beschikbaarheid van nutrienten in de bodem laag gehouden doordat met hooien nutrienten worden afgevoerd. Door de beperkte drainage kan er door indringende neerslag alleen een lichte verzuring van de bovengrond optreden. De veerkracht van deze ecosystemen ten opzichte van externe invloeden wordt ook in stand gehouden door een belangrijke positieve terugkoppeling in de voedselkringloop: tussen de effecten van de nutrientenbeschikbaarheid op de soortensamenstelling en de effecten van dominante plantensoorten op de mineralisatie van nutrienten. Indien deze veerkrachtmechanismen niet worden overbelast of verstoord, kunnen de stabiele bodem condities langdurig voortbestaan en kan er zich een soortenrijke blauwgraslandvegetatie ontwikkelen.

Na de beschrijving van deze referentie wordt, in het kader van deze evaluatie, aandacht besteed aan de respons van de bestudeerde blauwgraslanden op hydrologische veranderingen. In de Bennekomse Meent is een relatief beperkte en geleidelijke verandering in bodem en vegetatie opgetreden. In de andere studiegebieden waren deze veranderingen sterker, door een grotere afname van de kwel. In het blauwgrasland van het Korenburgerveen is een plotselinge toename opgetreden van zuurindicerende, soortenarme plantengemeenschappen. Het groeiende, zure mospakket resulteerde hier in een onomkeerbare verzuring van de bodem. De kleiige bodem van de Veenkampen is door drainage en bemesting zo sterk geeutrofieerd dat verschraling onmogelijk is geworden.

Tenslotte worden in hoofdstuk 7 de effecten van enkele herstelmaatregelen geevalueerd op achtereenvolgens de hydrologische eigenschappen, de bodem en de vegetatie van de bestudeerde schraalgraslanden.

Indien er voldoende kwel optreedt vanuit diepe watervoerende lagen, kunnen hydrologische maatregelen leiden tot het herstel van basenrijke kwel in de wortelzone. Voor twee van de onderzoeksgebieden (Bennekomse Meent en Veenkampen) geldt echter dat zij hiervoor te klein zijn. Zij hebben blijvend te maken met lage grondwaterstanden in de zomer en de verzurende werking van infiltrerende neerslag. Het conserveren van neerslagwater, in dergelijke kleine reservaten, bevordert de verzuring van de bovengrond en leidt niet tot verhoogde zomergrondwaterstanden. Hoge grondwaterstanden in de zomer kunnen weer bereikt worden door infiltratie met diep grondwater, zoals in de Veenkampen, maar dit zal gepaard blijven gaan met verzuring van de bodem door de overheersende wegzijging. Grootschalige conservering van neerslagwater in het hoogveengebied van het Korenburgerveen reservaat, resulteerde er in dat in de schraalgraslanden het hele jaar door hoge grondwaterstanden konden worden gerealiseerd.

Ik constateerde dat de mogelijkheid tot herstel van het zuurbufferend vermogen van de bodem afhankelijk is van de kwelintensiteit. Deze is relatief groot in de Bennekomse Meent en matig in het schraalgrasland van het Korenburgerveen; in de Veenkampen domineert de wegzijging. De langzame verzuring die plaatselijk in het blauwgrasland van de Bennekomse Meent is aangetroffen kan worden teruggedraaid als er weer hogere grondwaterstanden in de zomer worden gerealiseerd. Deze reversibiliteit kan optreden dankzij de hoge basenverzadiging en redoxcapaciteit van de bodem en dankzij de aanwezige kwel. Incidentele overstroming met eutroof, basenrijk oppervlaktewater is hier een veelbelovende optie ter bestrijding van de verzuring. Aangetoond werd dat ongewenste effecten van eutrofiering op de bovengrondse biomassaproductie en op de soortensamenstelling na ongeveer vijf jaar zijn verdwenen (Hoofdstuk 3). Plaggen, in combinatie met de afvoer van het neerslagoverschot, voorkomt dat er hysteresis optreedt tijdens het herstel van het zuurbufferend vermogen van licht verzuurde bodems, zoals die voorkomen in de Bennekomse Meent. Het verwijderen van de sterk verzuurde bovengrond is een eerste vereiste om voortgaande verzuring te bestrijden in gebieden waar kwel bijna is verdwenen, zoals in het schraalgrasland van het Korenburgerveen. Het maaien en afvoeren van de vegetatie (hooien), aansluitend op hydrologische maatregelen en plaggen, is essentieel tot behoud van voedselarme condities in reservaten. In intensief door landbouw gebruikte laagveengebieden kunnen de oorspronkelijke natte, voedselarme condities met deze maatregelen niet op korte termijn hersteld worden omdat de bodem tot op grote diepte irreversibel is veranderd.

De voorgestelde maatregelen kunnen, bij voldoende kwel tot in de wortelzone, de successie in blauwgraslanden naar plantengemeenschappen die indicatief zijn voor zure, droge of natte omstandigheden vertragen of omkeren. Anderzijds zal op natte plaatsen, waar de kwel is verdwenen, de successie verlopen in de richting van Kleine zeggen gemeenschappen, ondanks dat aanvankelijk na plaggen zich doelsoorten uit het blauwgrasland vestigden. Hoewel in laagveengebieden na vernatting en plaggen van voormalige landbouwgronden er zich blauwgraslandsoorten kunnen vestigen verwacht ik dat deze soorten er niet zullen blijven omdat de bovengrondse biomassaproductie weer zal toenemen en er een voortgaande verzuring plaatsvindt.

Dit onderzoek heeft meer inzicht gegeven in de dynamiek van blauwgraslanden en in de effectiviteit van enkele belangrijke beheersmaatregelen. Het laat zien dat voor het bepalen van het beheer een cyclisch planningsproces vereist is. Uitgaande van duurzame hydrologische condities en de effectiviteit van herstelmaatregelen kunnen dan de werkelijk te ontwikkelen, of te behouden, plantengemeenschappen en doelsoorten worden geselecteerd. Het volgen van de in deze studie beschreven sleutelprocessen is onmisbaar om de effectiviteit van de toegepaste maatregelen in de praktijk te kunnen beoordelen en het beheer eventueel aan passen.

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Ongeveer 40 studenten hebben, onder mijn begeleiding, hun afstudeeronderzoek gedaan in de Bennekomse Meent, de Veenkampen of het Korenburgerveen. Jullie rake opmerkingen, spitse vragen en resultaten hebben de koers van mijn onderzoek beinvloed. Onderzoeksresultaten van Nico Burgerhart, Gerlies Nap en Sanne Knol zijn in enkele hoofdstukken verwerkt. Het was een leerzame wisselwerking: we ontdekten dat iets pas duidelijk voor je is, als je het goed kan uitleggen.

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Curriculum vitae

Dirk van der Hoek werd geboren op 20 juli 1949 te Rotterdam. In 1967 behaalde hij het HBS-B diploma aan het Libanon Lyceum in diezelfde plaats en begon hij aan de studie Fysische Geografie aan de Universiteit Utrecht. In de doctoraalfase heeft hij de bijvaken bodemkunde en planologie gekozen en heeft hij een afstudeeronderzoek gedaan in de uiterwaarden van de Rijn. Bovendien heeft hij toen deelgenomen aan een oceanografische expeditie naar de Nederlandse Antillen. De universitaire opleiding heeft hij in 1973 afgesloten, inclusief een onderwijsbevoegdheid.

Van 1973 tot 1976 werd hij als wetenschappelijk ambtenaar aangesteld bij de Rijksuniversiteit te Utrecht met de opdracht een milieukartering uit te voeren van het Noorderpark en de Vechtstreek. In het laatste jaar was hij gedetacheerd bij de Provinciale Waterstaat van Utrecht en was hij tevens als docent aardrijkskunde werkzaam in het middelbaar onderwijs. In 1976 werd hij aangesteld als wetenschappelijk medewerker bij de vakgroep Natuurbeheer van de Landbouwhogeschool. Van 1988 tot 1991 was hij namens de toenmalige Landbouwuniversiteit als coordinator betrokken bij de interuniversitaire postdoctorale milieuopleiding UBM. Sinds 1991 is hij lid van de Commissie voor de milieu-effectrapportage. Momenteel verzorgt hij als universitair docent onderwijs bij de leerstoelgroep Natuurbeheer en Plantenecologie van Wageningen Universiteit. Hij heeft als onderzoeker en begeleider deelgenomen aan diverse extern gefinancierde onderzoeksprojecten op het gebied van de ecohydrologie. De resultaten van zijn eigen lange-termijn onderzoek, naar de effecten van maatregelen tot herstel van soortenrijke natte schraalgraslanden, zijn voor een deel gebundeld in dit proefschrift.

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