Long-term effects of drainage and initial effects of hydrological restoration on rich fen vegetation

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Abstract

Questions: What vegetational changes does a boreal rich fen (alkaline fen) undergo during a time period of 24 years after drainage? How is plant species richness affected, and what are the changes in composition of ecological groups of species? Is it possible to recover parts of the original flora by rewetting the rich fen? Which are the initial vegetation changes in the flora after rewetting? What are the major challenges for restoration of rich fen flora after rewetting? Location: Eastern central Sweden, southern boreal vegetational zone. Previously rich fen site, drained for forestry purposes during 1978-1979. The site was hydrologically restored (rewetted) in 2002. Method: Annual vegetation survey in permanent plots during a period of 28 years. Results: There were three successional stages in the vegetational changes. In the first stage there was a rapid (<5 years) loss of rich fen bryophytes. The second step was an increase of sedges and early successional bryophytes, which was followed by an increase of a few emerging dominants, such as Molinia caerulea, Betula pubescens and Sphagnum spp. After rewetting, there are indications of vegetation recovery, albeit at slow rates. Depending on, for instance, initial species composition different routes of vegetation change were observed in the flora after drainage, although after 24 years, species composition became more homogenous and dominated by a few species with high cover. Conclusion: Major changes have occurred after changes in the hydrology (drainage and rewetting) with a severe impact on the biodiversity among vascular plants and bryophytes. Several rich fen bryophytes respond quickly to the changes in water level (in contrast to vascular plants). The recovery after rewetting towards the original rich fen vegetation is slow, as delayed by substrate degradation, dispersal limitation and presence of dominant species.

Keywords: Bryophyte; Long-term study; Mire; Rewetting; Succession; Wetland restoration.


Introduction

Sweden is the country within the European Union with the largest area of rich fens (ca. 100 000 - 150 000 ha or 2-3% of the total land area; Sundberg 2006). Many of these rich fens have been affected by drainage during the last two centuries – during the 19th century mainly for agricultural purposes and during the 20th century for forestry (Vasander et al. 2003). Ca. one million ha of the peatland area in Sweden have been drained for forestry and at a rough estimate equally large areas have been drained for agriculture (Rydin et al. 1999).

Drainage may alter the peat chemistry (for example lowered pH and leakage of cations; see Nauke et al. 1993) and biological attributes (invasion of dominant species) as a result of the combination of lowered water table and peat decomposition. The species composition may also respond to changes at the landscape level, such as altered water levels and outflow of groundwater in the surroundings (Grootjans & van Diggelen 1995; van Diggelen et al. 2006). Also, increased outflow of leached chemicals, for example Ca-ions, have been observed from drained peat (Nauke et al. 1993). Other factors, for example reduced management such as haymaking (Moën 1995), eutrophication and acidification (Sjors & Gunnarsson 2002) may also cause drastic changes in the rich fen flora. It has been suggested that vegetation changes after drainage in mire ecosystems resemble effects of global warming (Laine et al. 1995). The effect of drainage on mire vegetation has been reported to be more drastic in minerotrophic than in ombrotrophic sites (Heikkilä & Lindholm 1995). Concerning acidification, the effects are more obvious in less buffered systems (Wheeler & Shaw 1995) and, hence, these effects are more pronounced in moderately rich fens than in extremely rich fens with higher buffering capacity (high concentration of calcium), and the effects are also small in naturally acid poor fens and bogs (Gunnarsson et al. 2000).

Rich fens are very important from a conservation point of view and act as biodiversity hotspots in the landscape (Wassen et al. 2005; van Diggelen et al. 2006).
Rich fens contain a large proportion of threatened species of various groups of organisms (including vascular plants, bryophytes, land snails and insects). 160 rich fen species occur in the Swedish Red list and among these 74 are considered as threatened (Gårdenfors 2005; Sundberg 2006). Even moderate hydrological changes in these ecosystems may have a drastic, negative impact on the biodiversity, not least among vascular plants and bryophytes, but continuous, long-time monitoring of these processes are still lacking.

The recent interest and focus on restoration of mires (Pfadenhauer & Klötzli 1996; Pfadenhauer & Grootjans 1999; Vasander et al. 2003) also necessitates evaluations of the vegetation – will the mire vegetation recover and how long will it take? Several restoration studies have been performed in wetland ecosystems in western/central Europe (for a review see Pfadenhauer & Klötzli 1996), but the dissimilarities in wetland types and species composition often make comparisons with Nordic mire ecosystems difficult. A long-term study was performed in a fen meadow affected by drainage in The Netherlands (Grootjans et al. 2005), with low similarities in species composition to rich fens in the Nordic countries. Even though there are large mire areas in the Nordic countries that are directly or indirectly highly influenced by drainage, only few scientifically evaluated restoration projects have been carried out in these countries (although several studies of vegetation changes after drainage have been performed; see Backéus 1981). There is a big need for restoration of rich fens from a national point of view; 67 % (1067 objects) of the highest classed rich fens in the Swedish wetland inventory are affected by drainage (Sundberg 2006). There is also a need for long-term vegetation monitoring, not only for vascular plants but also for bryophytes, since the latter are often better indicators of changed mire hydrology than are vascular plants.

Comparison of drainage and restoration effects across regions is facilitated if studies are based on ecological groups, rather than on individual species. The use of functional groups has been discussed extensively during recent years, including their use in different biotopes and vegetation systems (for example Smith 1997), their usefulness for vegetation and biodiversity monitoring (Rusch et al. 2003) and for management and restoration (Hobbs 1997; Brown 2004). We use a similar approach and describe the changes in ecological groups of species, based on life form and affinity to rich fens.

In this study, we investigated the immediate and long-term post drainage floristic responses in permanent plots in a rich fen in central Sweden during a period of 24 years with the aim to document time scales of changes in species composition and in abundance of characteristic rich fen species and other ecological groups. Thereafter, we hydrologically restored (re-wetted) the fen and followed the vegetation changes during four years to test if the vegetation reverts back towards original composition, and, if so, at what rate.

**Material and Methods**

**Drainage and restoration experiment**

The study site is in Gästrikland (east central Sweden; 60°51’ N, 17°10’ E), i.e. in the southern-boreal vegetation zone (Sjörs 1999). The mean temperature for the nearest meteorological station (Gävle-Åbyggeby) for January is −5.1°C and for July 15.4°C, and the annual precipitation is 642 mm (Anon. 2005). The whole mire complex, including the rich fen parts which are the focus of this study, was drained for forestry purposes during 1978-1979 with one main ditch (1 m deep, 2 m wide) and several smaller feeder ditches which all drain into a small lake north of the study site. The bedrock in the area is acidic, but the morainic soils in this coastal area are influenced by calcareous material from nearby bedrock in the Bothnian Bay that was deposited here during the last glaciation. This calcareous material noticeably influences the minerotrophic waters passing into the mire and also influences the ecological properties of the mire vegetation. No water-chemical data from the pristine mire stage are available. The pH in the main ditch close to the plots was 6.4 (measured in May 2002) and the Ca concentration was 18 mg/l (measured in August 2005).

Still undisturbed mires in the vicinity of the experimental site contain moderately rich fen vegetation but also poor fens and bog communities. The vegetation before drainage was dominated in the wetter parts by brown moss species (mainly Amblystegiaceae s.l. such as Scorpidium spp. and Campylium stellatum) and sedges, such as Carex rostrata, C. panicea and C. livida.

Hydrological restoration by blocking of the main ditch was performed in December 2002. Blocking the main ditch was done at four positions (separated by a distance of 50 m) along the main ditch by establishment of a wooden dam in combination with peat and mineral soil that was compacted by an excavator 3 m upstream of the wooden dam. The altitudinal differences between adjacent dams did not exceed 20 cm. In the investigated part of the mire the water level rise after hydrological restoration was approximately 175 mm in a dip well 4 m from the ditch.

**Vegetation analysis**

Nine subplots (1 m × 1 m) were arranged in each of two plots (5 m × 5 m and 6 m × 10 m), ca. 10 m from...
the main ditch. Each plot was investigated annually in July-September 1979-1997 (except 1985 and 1996). The floristic monitoring was resumed in 2002 (before the hydrological restoration) and continued to 2006. One person (I. Backéus) took part in all vegetation analyses. All vascular plants and bryophytes were recorded, and their cover in percent was estimated according to the following scale: 0-1 %; 1-2 %; 2-3 %; 3-4 %; 5-10 %; 10-20%; 20-30% etc. The cover of the shrub layer (0.5-2 m) and tree-layer (higher than 2 m) was estimated five times during the investigation period (1979, 1984, 1989, 1995 and 2006) as vertical projection above each subplot.

Statistical analyses

Multivariate analyses were performed with the CANOCO software, version 4.51 (ter Braak & Šmilauer 2003). Detrended Correspondence Analysis, DCA, was used. Detrending was performed by segments with no further transformation of data. Average cover values of subplots were used for analysis of changes among all investigated years. For detailed ordination within 4 selected years, individual cover values for all subplots were used.

Classification into ecological groups

To evaluate the effects of drainage and restoration and facilitate comparisons with other studies (with a different set of species), the species were divided into nine ecological groups (Table 1) based on life form and affinity to rich fens in the region (for example Rydin et al. 1999).

<table>
<thead>
<tr>
<th>Rich fen sedges:</th>
<th>Herbs:</th>
<th>Other bryophytes:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carex livida</td>
<td>Cirsium palustre</td>
<td>Scorpidium scorpioides</td>
</tr>
<tr>
<td>Carex panicea</td>
<td>Drosera rotundifolia</td>
<td>Scoporia abbreviata</td>
</tr>
<tr>
<td>Rhynchospora fusca</td>
<td>Epilobium palustre</td>
<td>Distichium grandiflorum</td>
</tr>
<tr>
<td>Trichophorum alpinum</td>
<td>Equisetum fluviatile</td>
<td>Distichium orientale</td>
</tr>
<tr>
<td>Other sedges:</td>
<td>Galtia palustre</td>
<td>Sphagnum warnstorfii</td>
</tr>
<tr>
<td>Carex chordorrhiza</td>
<td>Hammarbya paludosa</td>
<td>Sphagnum capillifolium</td>
</tr>
<tr>
<td>Carex echinata</td>
<td>Menyanthes trifoliata</td>
<td>Sphagnum cuspidatum</td>
</tr>
<tr>
<td>Carex lasiocarpa</td>
<td>Potentilla erecta</td>
<td>Sphagnum fallax</td>
</tr>
<tr>
<td>Carex limosa</td>
<td>Ranunculus flammula</td>
<td>Sphagnum platyphillum</td>
</tr>
<tr>
<td>Carex nigra</td>
<td>Selaginella selaginoides</td>
<td>Sphagnum repens</td>
</tr>
<tr>
<td>Carex rostrata</td>
<td>Solidago virgaerea</td>
<td>Sphagnum subulatum</td>
</tr>
<tr>
<td>Eriophorum angustifolium</td>
<td>Tridentalis europaea</td>
<td>Sphagnum warnstorfii</td>
</tr>
<tr>
<td>Eriophorum vaginatum</td>
<td>Utricularia intermedia</td>
<td>Sphagnum warnstorfii</td>
</tr>
<tr>
<td>Rhynchospora alba</td>
<td>Viola palustris</td>
<td>Sphagnum warnstorfii</td>
</tr>
<tr>
<td>Grasses:</td>
<td>Viola riviniana</td>
<td>Sphagnum warnstorfii</td>
</tr>
<tr>
<td>Calamagrostis canescens</td>
<td>Viola riviniana</td>
<td>Sphagnum warnstorfii</td>
</tr>
<tr>
<td>Deschampsia flexuosa</td>
<td>Viola riviniana</td>
<td>Sphagnum warnstorfii</td>
</tr>
<tr>
<td>Molinia caerulea</td>
<td>Viola riviniana</td>
<td>Sphagnum warnstorfii</td>
</tr>
</tbody>
</table>

Other species:

- Frangula albus
- Myrica gale
- Picea abies
- Pinus sylvestris
- Rhus idaeus
- Salix caprea
- Salix cinerea
- Salix myrsinfolia
- Vaccinium oxycoccus

Rich fen bryophytes:

- Brynum pseudotriquetrum
- Campylium stellatum
- Scorpidium cossonii
- Scorpidium scorpioides

Other bryophytes:

- Aulacomnium palustre
- Brachythecium sp.
- Dicranella cerviculata
- Mnium sp.

- Pellia sp.
- Pohlia cf. nutans
- Polytrichastrum longisetum
- Polytrichum commune
- Riccia sp.
- Splachnum sp.
- Warnstorfia exannulata

Rich fen Sphagnum:

- Sphagnum centrale
- Sphagnum contortum
- Sphagnum platyphillum
- Sphagnum subulatum
- Sphagnum subulatum
- Sphagnum warnstorfii

Other Sphagnum species:

- Sphagnum capillifolium
- Sphagnum cuspidatum
- Sphagnum fallax
- Sphagnum girgensohii
- Sphagnum papillosum
- Sphagnum squarrosum

<table>
<thead>
<tr>
<th>Table 1.</th>
<th>Species in the two plots divided into ecological groups based on life form and affinity to rich fens in the region.</th>
</tr>
</thead>
</table>

Results

A few species determined the major changes in species composition throughout the investigation period (Fig. 1). The decrease and local extinction of rich-fen bryophytes, mainly Scorpidium scorpioides in plot 1 and Campylium stellatum in plot 2 occurred rapidly after drainage. Following their decrease, several rich fen sedges increased. In both plots, C. panicea peaked at 5-10 years after drainage (Fig. 1).

At the final vegetation analysis before rewetting (2002), Molinia caerulea clearly dominated among the vascular plants. In plot 1, the species was absent in 1979, but covered > 50% in 2002. In plot 2, cover increased on average from 7% in 1979 to > 50 % in 1992. After hydrological restoration in December 2002, Molinia peaked in 2003 in Plot 1 and then decreased, while its reduction started already in 2003 in plot 2 (Fig. 1).

A unidirectional movement along axis 1 in the DCA ordination for each year can be seen (Fig. 2; Table 2). The changes were especially rapid in 1982-1985. The movement of the plots towards higher loadings along axis 2 in these DCA ordinations fairly well coincides with the major expansion phase of Molinia caerulea. For both plots, a reduction of the movement or even a minor transition back along axis 1 was observed after hydrological restoration.

In a second ordination, the within-plot floristic variation was evaluated at four selected years after drainage. Selected years were 1979 (first year after drainage), 1988, 1997 and 2006 (4 years after rewetting). Plot 1 initially had a uniform vegetation among all subplots (seen by the tight cluster of subplots of 1979 in the ordination; Fig. 3), dominated by Scorpidium scorpioides and a few
dominant sedges (C. rostrata, C. livida). This uniform vegetation diverged rapidly and intensely after drainage. In plot 2, the initial vegetation was more diverse (with several drier subplots and higher proportion of woody plants and grasses) and in this plot we see a convergence in the flora as time after drainage passes by (Fig. 3; Table 2).

The tree and shrub layers played a small role only during the first 5 years after drainage, but then shrubs expanded and peaked in 1995. As the birches grew taller they started to form an expanding tree layer and the shrub cover decreased (Table 3).

A considerable turnover of species occurred in the first 10 years after drainage. The species richness during the drainage period was highest in 1988. Species richness was higher in 2006 (4 years after rewetting) than in 1997 (before rewetting) (Table 4.).

Several similarities in the composition of ecological groups can be seen in the two plots (Fig. 4): early decline of rich fen bryophytes followed by expansion of woody species and rich fen sedges, and later their replacement by grasses. The invasion and expansion of Sphagnum and other bryophytes occurred only in plot 1.
Discussion

We saw drastic changes in the rich fen vegetation during the period of 24 years after drainage, and the changes occurred in a stepwise manner. Earlier studies stress the importance of detailed long-term, continuous studies in permanent plots of vegetation changes after drainage of mires (Silfverberg et al. 2005) and the lack of knowledge about restoration effects in drained forested mires (Heikkilä & Lindholm 1995). A long-term study of vegetation changes was performed in a fen meadow affected by drainage in The Netherlands (Grootjans et al. 2005). That study shows low similarities in species composition with rich fens in the Nordic countries, but there are several similarities in changes of ecological groups of plants on a community level.

In our study, a continuous, detailed description of the vegetation changes in a rich fen after drainage but also after rewetting is given over a time span that is unusual for permanent plot studies of any kind.

Table 2. Summary of properties of the axes in the DCA ordinations. Gradient lengths are given in S.D units. E/TI is the eigenvalue of the specific axis divided by the total inertia.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Figure</th>
<th>Data</th>
<th>No. of samples</th>
<th>No. of species</th>
<th>Total inertia</th>
<th>Axis no.</th>
<th>Gradient length</th>
<th>Eigenvalue</th>
<th>E/TI</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2a</td>
<td>All years, subplots averaged</td>
<td>22</td>
<td>67</td>
<td>1.870</td>
<td>1</td>
<td>4.749</td>
<td>0.844</td>
<td>0.451</td>
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<td></td>
<td>2</td>
<td>1.426</td>
<td>0.100</td>
<td>0.053</td>
</tr>
<tr>
<td></td>
<td>3a</td>
<td>Selected years, all subplots</td>
<td>36</td>
<td>48</td>
<td>4.120</td>
<td>1</td>
<td>5.078</td>
<td>0.912</td>
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<td></td>
<td>2</td>
<td>2.896</td>
<td>0.411</td>
<td>0.100</td>
</tr>
<tr>
<td>2</td>
<td>2b</td>
<td>All years, subplot averaged</td>
<td>22</td>
<td>50</td>
<td>0.887</td>
<td>1</td>
<td>2.017</td>
<td>0.490</td>
<td>0.553</td>
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<td>0.579</td>
<td>0.033</td>
<td>0.037</td>
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<tr>
<td></td>
<td>3b</td>
<td>Selected years, all subplots</td>
<td>36</td>
<td>34</td>
<td>2.267</td>
<td>1</td>
<td>3.489</td>
<td>0.782</td>
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<td></td>
<td>2</td>
<td>1.697</td>
<td>0.185</td>
<td>0.082</td>
</tr>
</tbody>
</table>

Table 3. Average cover ($n = 9$ in each plot) of shrub and tree layer (0.5 - 2 m and > 2 m, respectively) measured in percent, analysed in a vertical projection above each individual subplot.

<table>
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<tbody>
<tr>
<td>Plot 1</td>
<td></td>
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</tr>
<tr>
<td>Tree layer</td>
<td>0.3</td>
<td>0.3</td>
<td>0.5</td>
<td>9.2</td>
<td>12.6</td>
</tr>
<tr>
<td>Shrub layer</td>
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<td>0.0</td>
<td>7.5</td>
<td>26.0</td>
<td>4.7</td>
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<tr>
<td>Plot 2</td>
<td></td>
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</tr>
<tr>
<td>Tree layer</td>
<td>5.3</td>
<td>5.3</td>
<td>0.5</td>
<td>18.1</td>
<td>19.5</td>
</tr>
<tr>
<td>Shrub layer</td>
<td>0.0</td>
<td>2.6</td>
<td>6.6</td>
<td>10.7</td>
<td>1.4</td>
</tr>
</tbody>
</table>

Fig. 4. Vegetation composition divided into ecological groups of species at four different years during the investigation period (1979, 1988, 1997 and 2006).

Table 4. Species turnover at four occasions during the investigation period.

<table>
<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td>Plot 1</td>
<td></td>
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</tr>
<tr>
<td>Total number of species</td>
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<td>22</td>
<td>15</td>
<td>27</td>
</tr>
<tr>
<td>Number of original (1979) species remaining</td>
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<tr>
<td>New species in comparison to previous column</td>
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<td>13</td>
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<td>14</td>
</tr>
<tr>
<td>Plot 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total number of species</td>
<td>14</td>
<td>16</td>
<td>13</td>
<td>18</td>
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<tr>
<td>Number of original (1979) species remaining</td>
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<td>6</td>
<td>6</td>
</tr>
<tr>
<td>New species in comparison to previous column</td>
<td>-</td>
<td>9</td>
<td>4</td>
<td>7</td>
</tr>
</tbody>
</table>
Changes in dominance and species richness after drainage

The changes in species composition occurred in three major steps. The first step was a major decrease of several species (mainly brown mosses) during the initial 5 years after drainage, similar to the changes reported by Silfverberg et al. (2005). After this stage, we saw a stage of high species turnover and an increase of rich fen sedges (such as Carex panicea) and woody species (e.g. Myrica gale) in plot 2, which again declined after ca. 10 years. The third stage, with major emergence of dominants (Molinia and Betula), started at different times after drainage, but after almost 30 years the species composition was quite similar in the two plots.

The rapid loss of brown mosses is noteworthy from a biodiversity point of view and indicates the direct influence of aeration of the peat for these groups of species. The loss of brown mosses occurred during the first 5 years after drainage. These changes were most pronounced in the wettest parts, and species in these microhabitats have earlier been reported to be the first species to disappear after drainage (Laine et al. 1995). It is noteworthy that species richness peaked during the period of drainage, with the highest number found after about 10 years. At this stage, species from several groups of vascular plants and bryophytes did occur in the mire. Species from the pristine stage in combination with ruderal colonists and forest species all contributed to the high species richness, as has also been shown in other studies (Vasander 1987).

Spatial variation in effects

The difference in the vegetational change between the plots most probably reflects the fact that the surface of plot 1 initially was drier. The vegetation there was initially very homogeneous. The vegetation changes took different routes, mainly during the first period (1979-1997) after drainage, although the species composition and distribution between ecological groups converged later on. Spatial heterogeneity will always occur and may be promoted by an expanding shrub and tree cover. Knowledge of different routes and rates of changes after hydrological interaction is needed to understand in which phase of degradation the fen is. When this is understood, it is easier to suggest correct restoration measures.

In plot 1 the vegetation in the subplots diverged through time, while in plot 2 the subplots converged, which most probably reflects the different initial conditions. This indicates that different parts of individual mires may respond to drainage depending on initial species composition. The most drastic species turnover will be seen in the wetter parts, where the rich fen bryophytes dominate and respond directly to the lowered water table (see Rydin et al. 1999; Hedenäs & Kooijman 1996). These conditions also clearly promote the invasion and expansion of Sphagnum and Polytrichastrum (see below for their effects).

The emergence and expansion of dominant species

Molinia caerulea has been reported in earlier studies to expand in, for example, heathlands in western Europe as an effect of increased nitrogen availability, and it seems to be a dominant grass excluding other species (Berendsen & Elberse 1990). As shown in our study, the establishment of Molinia may take some time, but then the expansion is very rapid. Several studies have discussed the increase of Molinia, and the reasons therefore. Annual or biennial scything reduces Molinia (Moen et al. 1999) and dry periods are expected to lead to an expansion of the species (Boeye et al. 1999). This has been shown to be partly due to effective use of phosphorus in drier habitats in comparison with wetter sites (El-Kahloun et al. 2000). Molinia also has a wide pH tolerance (Taylor et al. 2001) and is classified as a stress tolerant competitor (Grime et al. 1988). Although we did not investigate the physiological explanation for the expansion of Molinia, our data indicate that it is a superior competitor under drier conditions in rich fens.

The effects on species diversity should also be discussed in relation to the increase of grasses and woody species, which probably caused decreased levels of light, increased litter accumulation and desiccation of the upper peat profile. Similar increase of grasses after drainage in combination with reduced species richness has been described from wetland ecosystems in The Netherlands (Grootjans et al. 2005). There, natural compaction of the peat layers led to rewetting some 16 years after drainage, which caused a decline of the dominant grasses. This is similar to the reduction of Molinia we found after the hydrological restorations.

Effects of expanding bryophytes

In plot 1, the initial great loss of brown mosses was later followed by an increase in other bryophytes, such as Pohlia nutans and Polytrichastrum longisetum (stress tolerant ruderals; cf. Grime 2002) that started after the decrease of rich fen sedges, approximately ten years after drainage. These bryophytes seem to be good colonizers that explore the bare peat surface of decaying brown mosses and sedges. The dominance by Polytrichastrum will prevent recolonization of other bryophytes due to their rapid spatial cover of bare peat patches. A similar succession of bryophytes has been reported from forested fens in Finland, where decreasing Sphagnum was
replaced by colonizers established by spores (for example Pohlia nutans) and then followed by forest floor species (Laine et al. 1995).

One major obstacle for the recovery of the vegetation is the increase of Sphagnum after rewetting in parts of the mire. These mosses will change the chemical properties of the water and surface and inhibit recolonization of brown mosses. One such expanding species is Sphagnum squarrosum, which has been reported to respond positively to increased levels of nutrients (Kooijman & Bakker 1995) and to replace species in minerotrophic mires after eutrophication and acidification. It is one of the first species that invade rich fens that have become drier and more acid (Hedenäs & Kooijman 1996). Several brown moss species (e.g. Scopridium scorpioides and Campylium stellatum), have the same pH range as Sphagnum squarrosum (Andrus 1986; Hedenäs 2003), but the presence of Sphagnum will gradually lower the pH further (Clymo 1963, 1964). Sphagnum hummocks may also overgrow the brown mosses (Kooijman et al. 1994).

**Restoration**

In addition to unsuitable chemistry and hydrology, restoration may be unsuccessful because of dispersal limitations. Since several rich fen specialists disappear in just a few years after drainage, natural establishments have to rely on long distance dispersal, dispersal from remnant populations in the surrounding mire, or from long-term persistent seed banks (Jensen 2004). Overcoming the dispersal distances by the use of transplantations of locally extinct species may be feasible (Mälson & Rydin 2007).

Restoration of rich fen vegetation depends on the severity of the damage (Grootjans & van Diggelen 1995), the time that has passed since drainage (as is clear from our results), the changes in chemical properties of the peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995). A eutrophicated peat and the possibilities to re-introduce (in our case Ca-rich) water (Heikkilä & Lindholm 1995).

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In summary, several actions may be needed for successful regeneration of the rich fen flora. Rewetting is the first step, and should preferably be more drastic than in this study. Removal, perhaps repeated, of dominant species (trees, shrubs, Molinia, Polytrichastrum, Sphagnum) in combination with surface peat removal, liming and reintroduction of rich fen specialists may also be necessary. Otherwise the substrate may once again degrade as an effect of invading dominants.

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