Water level fluctuations in rich fens: an assessment of ecological benefits and drawbacks
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CHAPTER 7

Synthesis: an assessment of ecological benefits and drawbacks

7.1 Introduction

For the proper functioning of endangered biodiverse rich fens, protected as EU priority habitat H7140A – Transition mires and quaking bogs (Quaking fens), base-rich and nutrient-poor (mesotrophic) conditions are required to prevent succession towards Sphagnum-dominated peatlands. Unfortunately, water- and soil quality of many European wetlands are negatively affected by changes in hydrology, eutrophication, acidification and toxicity, resulting in a decline in brown moss-dominated, biodiverse rich fens. During the past decades, water levels in European rich fen areas have often become constricted within narrow limits as a result of adjacent agricultural water management.

From a management perspective, the re-establishment of fluctuating water levels in non-pristine fens is considered, in order to optimize the generic ecological quality and to conserve and restore the vegetation in current brown moss-dominated rich fens. This chapter provides a synthesis, in which results and conclusions from the preceding chapters in combination with results from previous studies are discussed, summarized and integrated in an overview of potential ecological benefits and drawbacks from a management perspective (Figure 7.1).

The research was primarily focused on the biogeochemical effects of water table fluctuations in peat soils, as induced by changes in the surface water level, and their interaction with plant development. The effects of water table fluctuations were tested for different fen types, since biogeochemical soil characteristics may largely differ among different fen types, as influenced by surface water and/or current or former discharge of groundwater. Soil Ca- and Fe-contents turned out to be very important, and therefore a general distinction is made in this synthesis between Ca-rich fens with Fe-poor soils (soil Ca-content > 240 mmol kg\(^{-1}\) d.w., soil Fe-content < 35 mmol kg\(^{-1}\) d.w.; representative for rich fens in the Dutch peatland area Weerribben-Wieden) and rich fens with lower soil Ca content, but Fe-rich soils (soil Ca-content < 190 mmol kg\(^{-1}\) d.w., soil Fe-content > 180 mmol kg\(^{-1}\) d.w.; representative for rich fens in the Dutch peatland area Oostelijke Vechtplassen). Also the differences in responses among different vegetation types were tested, in particular between brown moss-dominated rich fen vegetation and Sphagnum-dominated vegetation. In addition, water quality appeared to be an important factor, especially when fens are inundated from time to time. Therefore, different water qualities
### Figure 7.1 A summarizing overview of potential benefits and drawbacks of lowered and increased surface water levels, and hence changes in water tables in rich fen peat soils, on the level of site conditions (based on, and reformulated from Mettrop et al., 2012; Cusell et al., 2013; Cusell, 2014).

<table>
<thead>
<tr>
<th>Lowered water levels</th>
<th>Increased water levels</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Benefits</strong></td>
<td><strong>Drawbacks</strong></td>
</tr>
<tr>
<td>• Aerobic oxidation results in acidification</td>
<td>• Fe(III) reduction induces net P-mobilization</td>
</tr>
<tr>
<td>- Only during long-term drought (&gt; 7 weeks)</td>
<td>- Especially when vegetation development is limited</td>
</tr>
<tr>
<td>- Particularly in Fe-rich soils</td>
<td>- Only in Fe-rich soils with high P-contents</td>
</tr>
<tr>
<td>• Fe(II) oxidation induces P-immobilization</td>
<td>- Fe(III) reduction in S-rich soils via formation of FeSx</td>
</tr>
<tr>
<td>- Only in Fe-rich soils</td>
<td>- External eutrophication</td>
</tr>
<tr>
<td>- Vascular plants are still capable of taking up immobilized P</td>
<td>- Only in case of P- and/or N-rich supply water</td>
</tr>
<tr>
<td>• Increased germination and establishment of plants</td>
<td>• Reduction may result in NH₄⁺, H₂S or Fe(II) toxicity</td>
</tr>
<tr>
<td>- Increased porewater nutrient concentrations and toxicity in porewater may be prevented by increased uptake by plants</td>
<td>- Especially when vegetation development is limited</td>
</tr>
<tr>
<td>• Biodiversity decreases</td>
<td>- NH₄⁺ concentrations particularly increases with P-rich supply water in Fe-rich fens</td>
</tr>
<tr>
<td>- Establishment and development of only fast-growing spp.</td>
<td>- Only in case of P-rich supply water in Fe-rich fens</td>
</tr>
<tr>
<td>- Drought-stress for characteristic rich fen spp. (e.g. Scorpidium)</td>
<td></td>
</tr>
<tr>
<td>• Soil subsidence is enhanced</td>
<td></td>
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<tr>
<td>- Especially when vegetation development is limited</td>
<td></td>
</tr>
</tbody>
</table>

| • ANC can be improved by inundation | • Competition by fast growing spp. is limited |
| - Only in case of base-rich, nutrient-poor surface water | |
| - Only when peat layer is attached to the underlying substrate | |
| - Only during summer inundations | |
| - Only in rich fens, not in Sphagnum-fens | |
| - Alkalization is temporary, Ca-supply may be more lasting | |

- **Moderate drought increases net N-mineralization**
  - Only in rich fens, not in Sphagnum-fens
- **Severe desiccation increases P-availability & DOC**
were included in the water level manipulation experiments. The potential benefits and drawbacks described in this synthesis are primarily based on the impact of fluctuating water levels on the environmental constraints as elucidated in Chapter 1. Following on from this, implications and recommendations are presented for different fen types to support water and nature management authorities in decision-making.

7.2 Higher incidence of lowered water levels

Potential benefits

Temporary drought may have a beneficial limiting effect on phosphorus (P)-availability, but this is highly dependent on the chemical composition of the peat soil. In rich fens with Fe-rich soils, temporary drought may be beneficial for P-limited vegetation types to some extent, since high rates of Fe-oxidation and subsequent Fe-P precipitation in the soil (Patrick and Khalid, 1974; Richardson, 1985) can temporarily reduce P-availability in porewater. Fe-related precipitation of P from the surface water can be important for development of aquatic vegetation in open water by the reduction of algal development, and hence for the rejuvenation of early stages of terrestrialization. However, in the context of preserving current rich fens, Fe-related P-immobilization in the soil may have totally different effects. As elucidated in Chapter 6, total soil Fe-content in rich fens is positively correlated with total soil P-content and P-concentration in plant tissue, and negatively correlated with foliar N:P ratios in vascular plants. In the most Fe-rich fens, N:P ratios were even below 13.5 g g⁻¹, indicating potential nitrogen (N)-limitation and excess of P. This remarkable positive correlation between soil Fe-content and P-availability contrasts the idea that high Fe-contents automatically lead to low values of plant-available P. Being true for the surface water in aquatic systems, this does not hold for peat soils in rich fens. Instead, high groundwater Fe discharge may lead to the accumulation of P that is still available to plants due to the relatively weak binding of P within abundant Fe-OM (Organic Matter) complexes. Enhanced P-immobilization during temporary droughts in Fe-rich fens is therefore not necessarily beneficial, which is not only an important finding from a management perspective, but moreover of great interest in terms of the general understanding of biogeochemical processes in peatlands. In addition, Ca-rich fens with low Fe-contents do not show a response in porewater P-availability to increased oxygen availability, because immobilization of P by co-precipitation with calcite is not induced or affected by aerobic conditions.

Aerobic oxidation during aeration can result in detoxification of NH₄⁺, sulfide and Fe(II). Especially after a long period with anaerobic conditions, NH₄⁺ concentrations can decrease during episodes with lowered water tables. For rich fen
bryophytes, known to be sensitive to NH$_4^+$ toxicity (Paulissen et al., 2004; Verhoeven et al., 2011), occasional oxidation-induced detoxification may therefore be important.

In addition, a period of drought early in the growing season can considerably stimulate germination and establishment of vascular plants, leading to reduced porewater nutrient concentrations. Increased plant development, and hence increased plant activity, probably leads to increased radial oxygen loss (ROL) from roots (Lamers et al., 2012), stimulating nitrification in the rhizosphere, and increased uptake of N. Also P-consumption by plants can be strongly enhanced by increased growth rates in early spring. This can tone down the stimulating effect of P-availability on microbial activity (Amador and Jones, 1995; White and Reddy 2000), and hence mitigate toxicity of NH$_4^+$, Fe(II), sulfide and/or organic acids.

In addition to the effects on the level of site conditions as shown in Figure 7.1, surface water level fluctuations can have a major impact on a landscape scale. Allowing lowered surface water levels can result in a reduced need for external input of nutrient-rich water in the entire wetland (Coops and Hosper, 2002; Jaarsma et al., 2008; Schep et al., 2012). This is actually not a direct drought-induced effect, but primarily an effect of hydrological isolation. Moreover, this effect is strongly dependent on area-specific hydrological conditions and water quality. In De Weerribben, for instance, a short period in summer with water level drawdown of about 5 cm, did not seem to affect flow rates, flow directions and the chemical composition of surface waters (Cusell, 2014).

**Potential drawbacks**

One of the main risks with regard to drought is the stimulation of aerobic oxidation processes, which may lead to decreased soil acid neutralizing capacity (ANC) (Stumm and Morgan, 1996), and subsequently to vegetation changes. Also this effect strongly differs among fens with different biogeochemical characteristics. In Ca-rich fens with low soil Fe-contents, the effects of drought-induced oxidation and acidification are small, because Ca is not redox sensitive and changes in pH can be buffered (Stumm and Morgan, 1996). In rich fens with Fe-rich soils, however, acidification can be enhanced by Fe(II) oxidation, and hence pH values can drop to values below 6.0 after a drought period of 10 weeks, which is considered a critical pH value for rich fens dominated by brown mosses (Kooijman, 2012). During short-term drought (7 weeks), however, ANC remained sufficiently high in both rich fen types to prevent a severe drop in pH.

Lowering of pH as a result of a lowered water table is assumed to be temporary. When the water table is increased again, most of the protons produced are consumed due to the anaerobic reduction of alternative electron acceptors. However, a temporary decrease in pH may lead to suitable conditions for dominance by Sphag-
num-species that further acidify the habitat, which in turn can lead to severe decline of the rich fen bryophyte vegetation.

As a result of moderate drought of about 10 weeks, in which only the oxygen availability increases but the peat soil remains moist, carbon respiration rates can increase, but only in rich fens and not in Sphagnum-dominated fens. In the latter fen type, decomposition is probably not only limited by oxygen deficiency, but also by the high concentrations of phenolic compounds in Sphagnum-litter (Van Breemen, 1995; Aerts et al., 2001). Rich fens presumably contain lower concentrations of phenolic compounds. Also, the low pH in Sphagnum-fens may have been relatively unfavorable for the degradation of phenolic material (Pind et al., 1994). In rich fens, stimulation of phenol oxidase activity by aeration may therefore lead to phenol-concentrations that are low enough for other degradative enzymes in rich fens to be active, such as glucosidase and phosphatase (Freeman et al., 2004), resulting in increased respiration upon aeration in rich fens.

An important question with respect to vegetation is: does this increase in decomposition rates upon 10 weeks of aeration in rich fens also result in increased nutrient availability? Aeration only resulted in increased net N-mineralization in rich fens. Net N-mineralization rates in Sphagnum-fens were, however, not affected by increased availability of oxygen, which is attributed to differences in concentrations of phenolic compounds and degradative enzymes, like for respiration. No significant differences in net P-release were detected during aeration, even though respiration rates increased. This may be caused by the fact that released P can be bound immediately after mineralization, for example as Fe-phosphates or Ca-phosphates. Especially the formation of Fe(III) oxides in rich fens with Fe-rich soils may reduce net P-mobilization during aeration, as explained in the previous section.

Upon severe drought of about 10 weeks, i.e. total desiccation, DOC production increased considerably, which may be related to die-off of microbes as a result of water shortage, by which cellular constituents are released. This idea was indeed supported by a decreasing microbial C mass upon total desiccation. In contrast to aeration, full desiccation led to an enormous increase of net P-release. High microbial mortality resulting from drought, as supported by the reduced microbial biomass C upon desiccation, may have resulted in a net increase of extractable o-PO4 concentrations.

A high drought incidence can also have direct effects via drought stress in vascular plants and bryophytes. As a result, typical wetland plant communities may be replaced by vegetation favored by drier conditions (Lamers et al., 2015). Since rates of N-mineralization and P-immobilization by Fe(III) compounds both increase, the encroachment of dryland graminoid species may be stimulated at the expense of characteristic brown moss and slow-growing vascular species (Verhoeven et al., 2011; Cusell et al., 2014). Subsequently, increased biomass production can lead to a
less diverse species composition and may offer less room and light for rich fen mosses. In addition, drought may lead to favorable conditions for *Sphagnum* spp. at the expense of brown mosses. While *Sphagnum* spp. are well able to tolerate both water shortages and acid conditions (Rochefort et al. 1990), vitality of brown mosses such as *Scorpidium* spp. strongly decreases during 7 weeks of drought.

Drought can also lead to subsidence of the peat soil surface, particularly when preceded by inundation. This suggests that subsidence is not solely due to reduced buoyancy by release of entrapped gas bubbles (Strack et al., 2006), or increased decomposition rates as a result of aeration. Presumably, subsidence is further induced by the reduced vegetation development during prior inundation, which led to inhibited root growth and lower stability of the peat soil.

**Lowered water levels: conclusions and implications for management**

All in all, the potential drawbacks seem to be more important than the potential benefits of temporary lowered surface water levels, and related lowered water tables in the peat soil. The combined effects of enhanced acidification (particularly in Fe-rich soils), increased nutrient mineralization, direct drought-stress for brown mosses, improved conditions for *Sphagnum* spp., and increased biomass production by fast-growing species will strongly hamper the development of protected brown moss vegetation in rich fens. A drought-induced vegetation shift from rich fen vegetation (H7140A; Figure 1.1) to *Sphagnum*-dominated fens (H7140B), as described in Chapter 1, poses a major threat for the conservation of rich fen biodiversity. Long-term (>7 weeks) aeration and especially desiccation of the top 10 cm of the soil in rich fens should therefore be avoided.

**7.3. Higher incidence of increased water levels**

**Potential benefits**

In terms of counteracting acidification of rich fens, shallow short-term summer inundation with base-rich surface water can be an efficient measure. In contrast to winter inundation, raising surface water levels in summer, when evapotranspiration rates are high, results in infiltration, and hence an increase of ANC. Secondly, internal alkalinity generation, as a result of anaerobic microbial redox processes (Stumm and Morgan, 1996), is enhanced by higher temperatures in summer. The latter effect will be temporary, since aerobic oxidation during subsequent droughts can lead to re-acidification. The first process of infiltration of Ca-rich water, however, may contribute to a lasting increase in the peat soil ANC, as the ANC is not only determined by the amount of bicarbonate in porewater in the circum-neutral pH range, but also by the saturation of Ca and Mg at the adsorption complex in the pH
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range below (Stumm and Morgan, 1996). The ability of rich fen soils to exchange H\(^+\) for Ca\(^{2+}\) from the adsorption complex, and thereby buffer porewater pH, will be highly beneficial to counteract acidification during subsequent periods of drought in particular, when bicarbonate has been largely consumed and base cation exchange against H\(^+\) initiates.

In *Sphagnum*-dominated fens, however, ANC remains relatively low during summer inundation with base-rich surface water, presumably due to exchange of Ca\(^{2+}\) from inundation water for H\(^+\). In addition, *S. palustre* is well able to endure periods of inundation. Even with base-rich inundation water, which was assumed to cause problems since *Sphagnum* spp. are generally associated with and adapted to acidic conditions, *S. palustre* thrived remarkably well. Short-term summer inundation with base-rich water as a measure seems therefore only efficient in places where base-rich conditions still prevail. At the point when *Sphagnum* spp., which are able to acidify its environment, have already made their entry over a large surface area, short-term inundation is less effective. Therefore, short-term summer inundation is primarily considered a preventive measure, in order to maintain current brown moss-dominated rich fens.

Short-term summer inundation as a measure is, however, only considered beneficial under specific conditions. First, raising the surface water level has the strongest effect when the peat layer is attached to the underlying substrate by roots, because otherwise inundation is difficult due to peat buoyancy. Raising water levels in ditches and canals without actual inundation will only gradually affect the fens, and often only increases ANC in the first couple of meters as lateral water movement through the peat soil is very slow due to its low hydrological conductivity (Lamers et al., 2015). In floating *Sphagnum*-dominated fens, raising surface water levels does not result in inundation, because the buoyant peat follows changes in surface water levels and the water table in the peat soil remains unaltered. This, however, may be different in floating rich fens. As shown by aerial footage of the National Park Weerribben-Wieden (Cusell, 2014), inundation of floating rich fens with *Scorpidium* spp. is not uncommon. In the case of floating rich fens, the origin of inundation water and the mechanism by which inundation takes place is still subject to debate. In young fens, seepage from beneath the floating peat mat may be involved, but in later stages, flooding of surface water from adjacent ditches over the peat mat is more likely. Since these questions are relevant for management, it is important that further research is conducted on flooding in floating rich fens.

Inundation may have additional effects on vegetation development. A wet period in early spring, resulting in reduced vegetation development, is not necessarily detrimental for mesotrophic peatlands. Competition by fast growing species may be limited this way, which may eventually result in increased biodiversity. In addition, inundation, or at least waterlogging, turned out to be vital for rich fen bryophytes.
Potential drawbacks
During inundation, P-availability may increase as a result of net P-mobilization (internal eutrophication) due to Fe reduction (Patrick and Khalid, 1974). Especially in Fe-rich soils with high P-contents, this rapid anaerobic P-mobilization can be severe. Moreover, high sulfate reduction rates and formation of iron sulfides (FeSx) may lead to decreased P-binding capacity of the peat sediment, and hence additional P-mobilization in S-rich soils (Caraco et al., 1989; Smolders and Roelofs, 1993; Lamers et al., 1998). This net internal P-mobilization may be lower upon inundation after a period of several weeks of drought in spring, as a result of increased growth rates and P-consumption by plants. In rich fens with high Ca-contents, however, net P-mobilization during inundation is relatively low. This can be explained by the fact that most P is bound to Ca, which is not sensitive to oxidation-reduction processes (Stumm and Morgan, 1996).

Increased surface water influence, as a result of inundation, can also lead to higher nutrient inputs (external eutrophication) (e.g. Koerselman and Verhoeven, 1992; Wassen et al., 1996). In relatively nutrient-poor (mesotrophic) fens adjacent to agricultural areas, external P-input can be highly detrimental (Lamers et al., 2015). This effect may also strongly depend on biogeochemical characteristics of the peat soil, in which particularly a high soil Ca-content, and to a lesser extent a high Fe-content, can be beneficial because of P-immobilization.

Anaerobic conditions can also lead to the formation of potential phytotoxins such as NH4+, sulfide, Fe(II) and/or organic acids to plants, depending on soil chemistry (Lamers et al., 2015). Plant growth can strongly be hampered during inundation in early spring shortly after winter, when the vegetation has had little chance to develop and ROL is still low, due to accumulation of these toxins. In Fe-rich fens, inundation with P-rich water can lead to porewater Fe-concentrations over 1000 µmol L⁻¹, and NH₄⁺ concentrations well over 100 µmol L⁻¹, a level above which toxic effects can seriously damage bryophyte vegetation under summer conditions (Paulissen et al., 2004; Verhoeven et al., 2011). In Ca-rich fens, the relatively high pH presumably stimulates nitrification in the topsoil (Wild et al., 1971), and NH₄⁺ concentrations generally do not exceed 100 µmol L⁻¹ (e.g. Rochefort and Vitt, 1988; Kooijman and Westhoff, 1995).

Increased water levels: conclusions and implications for management
In contrast to drought, periods of inundation with base-rich water in summer can be favorable in order to structurally improve the porewater ANC. Both supply of base-rich water and internal soil alkalization in the topsoil of Ca-rich fens that lack sufficient HCO₃⁻ and Ca-buffering can be important to prevent acidification. In rich fens with Ca-rich soils and low Fe-contents, the potential benefits of temporary inundation outweigh potential drawbacks, since short-term inundation is
not harmful in terms of P-mobilization. In rich fens with Fe-rich soils, however, inundation should be prevented shortly after winter, when vegetation development, hence P-consumption by plants, is still limited. Especially inundation with P-rich water seems to stimulate microbial activity, despite Fe-related precipitation of P, resulting in NH₄ and/or Fe(II) toxicity. For Fe-rich fens in agricultural areas, this may well generate a friction between preventing acidification and N-eutrophication during drought on the one hand, and preventing external eutrophication and accumulation of toxins during inundation on the other hand. Therefore, improved water quality is a primary requirement in these fens.

7.4 Concluding remarks

This synthesis identifies the potential benefits and drawbacks of re-establishment of fluctuating water levels in non-pristine fens in order to conserve and restore the vegetation in current brown moss-dominated, biodiverse rich fens. Area-specific chemical properties of peat soils and surface water, as determined by the geohydrological setting in the landscape, turned out to strongly determine the responses to surface water level-induced water table fluctuations in the peat soil. Especially the Ca- and Fe-contents of peat soils proved to be very important factors. In addition, the timing of temporary drought or inundation in the growing season turned out to be important, because of the strong interaction between biogeochemical processes and vegetation development. These findings not only contribute to the general biogeochemical and ecological understanding of water level-induced processes in rich fens, but are also valuable to support water and nature management authorities in decision-making.

References


