Water level fluctuations in rich fens: an assessment of ecological benefits and drawbacks
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1.1. Rich fens

A rich fen is a mire type that is characterized by base-rich and nutrient-poor (mesotrophic) conditions (Sjörs, 1950; Van Wirdum, 1991; Kooijman, 1993; Wheeler and Proctor, 2000). The term ‘rich’ not only refers to the high concentrations of minerals, but also to the high floristic diversity (Wassen et al., 2005; van Diggelen et al., 2006). The vegetation composition in rich fens (Scorpidio-Caricetum diandrae) strongly depends on sufficient supply in the topsoil of mineral-rich surface water and/or groundwater, which has been in contact with base-rich substrates (Gore, 1983; Van Wirdum, 1993; Wheeler and Proctor, 2000). As a consequence, rich fens harbor a large number of threatened minerotrophic vascular plant species and brown mosses, which depend on relatively high acid neutralizing capacity (ANC), high pH, and low nutrient availability.

Rich fens have become very rare in densely populated and heavily exploited landscapes, and are therefore protected as EU priority habitat H7140A – Transition mires and quaking bogs (Quaking fens), which is one of the different peatland habitat types as differentiated within Natura 2000 legislation. The distinction between many Natura 2000 wetland habitat types is based on different successional stages in the encroachment of open water by vegetation (terrestrialization), which is to a great extent determined by successive biogeochemical conditions and processes (Tallis, 1983). With respect to the conservation and management of rich fens, it is therefore important to focus on the processes that are involved in this terrestrialization process.

The earliest stage of this succession is characterized by aquatic vegetation such as Chara spp. in small open water bodies (habitat type H3140; Figure 1.1). In this phase, only small amounts of organic matter have accumulated yet and mineralization rates are low (Koerselman and Verhoeven, 1992). Stratiotes aloides L., with its sturdy leaves, may facilitate further encroachment by providing physical support and is considered an important constituent of the next step in succession (Sarneel et al., 2011; Harpenslager et al., 2015), leading to habitat type H3150. As a result of further hydrosere succession, floating root-mats are formed, which stay in direct contact with the minerotrophic surface water. Since microbial decomposition is still slowed down under these waterlogged, anaerobic conditions, dead remains of constituent plants gradually accumulate, and formation of peat is initiated (Tallis, 1983). This relatively thin, base-rich but nutrient-poor peat layer provides the
required conditions for development of rich fens (Habitat type H7140A) and their characteristic bryophytes such as *Scorpidium scorpioides* (Hedw.) Limpr., *Scorpidium cossonii* (Schimp.) Hedenäs, and *Hamatocaulis vernicosus* (Mitt.) Hedenäs, also referred to as brown mosses. For preservation of rich fens, it is essential that the surface layer stays in direct contact with minerotrophic, base-rich water. Once the peat growth exceeds the minerotrophic water layer and peat deposits become isolated, the influence of poorly buffered rainwater becomes bigger (ombrotrophic conditions), which leads to a decreased ANC and formation of peat bog vegetation (H7140B) (Van Wirdum, 1991; Koerselman and Verhoeven, 1992; Van Diggelen et al., 1996). In addition, aerobic conditions and hence oxidation processes, in which oxygen is used as a terminal electron acceptor, lead to acidification (Stumm and Morgan, 1996), which in turn results in reduced ANC. Development of habitat type H7140B is a relatively rapid process that is accompanied by the invasion of *Sphagnum* species (Bellamy and Rieley, 1967; Tállis, 1983; Kuhry et al., 1993; Laine et al., 2011). Since *Sphagnum* species release protons in exchange for other cations (Clymo, 1963; Kooijman and Bakker, 1994), acidification of the rich fen bryophyte layer is intensified (Van Wirdum et al., 1992). The increased gradual loss of contact with minerotrophic water, increased peat accumulation by *Sphagnum*, and further succession leads to development of wet heaths, defined as habitat type H4010B.

In the Netherlands, where both fens and bogs were exploited for fuel since medieval times, but particularly during the 18th and 19th centuries, these different wetland habitat types successfully developed in residual peat excavation turbaries (Van Wirdum et al., 1992; Vermeer and Joosten, 1992). However, during the past 50 years, the hydrosere succession by vegetation in open water is inhibited (Lamers et al., 2002), resulting in absence of rich fen rejuvenation. In addition, transition from rich fens to bogs is enhanced, resulting in deterioration of present rich fen habitats.
Consequently, rich fens dominated by *S. scorpioides*, *S. cossonii* and *H. vernicosus* have become very rare in the Netherlands (Kooijman, 1992; Paulissen et al., 2013; Cusell, 2014a). Also other countries in Western Europe show serious deterioration of brown moss-dominated rich fens over the past decades (JNCC, 2007).

1.2. Environmental constraints

The major constraints on the conservation and restoration of rich fens in agricultural areas in Europe are considered to be acidification, eutrophication and toxicity, next to direct drought effects on communities (e.g. Lamers et al., 2015). All of these environmental constraints are induced by anthropogenic disturbance.

**Acidification**

The cause of acidification lies in several different processes. Hydrological isolation from base-rich groundwater and surface water, caused by natural succession and/or anthropogenic intervention, has led to reduced ANC in fen peatland regions with intensive agriculture (e.g. van Wirdum, 1991; Van Diggelen, 1996). Presumably, increased atmospheric N-deposition as a result of fossil fuel combustion and intensive cattle farming has exacerbated the acidification of fens due to direct influx of nitric acid and sulfuric acid, and indirectly by additional ammonium oxidation (nitrification) and sulfide oxidation during periods of drought (Gorham et al., 1987; Lamers et al., 2015). Finally, the shift from base-rich bryophytes to *Sphagnum* spp. may lead to further acidification, since *Sphagnum* spp. can release protons in exchange for other cations (Clymo, 1963; Kooijman and Bakker, 1994).

**Eutrophication**

The term eutrophic refers to relatively high availability of primary nutrients, and eutrophication refers to the increased availability of elements limiting primary production in an ecosystem. In general, eutrophication causes the disappearance of characteristic slow-growing plant species and bryophytes, because they are outcompeted by strongly competitive, faster growing and generally more common species, leading to biodiversity loss (Wheeler and Shaw, 1991). In the case of rich fens, rapid succession towards poor fens or bogs (habitat type H7140B; Figure 1.1) is enhanced. So, to conserve the present brown moss-dominated rich fens, site conditions should be characterized by a relatively low nutrient availability (Kooijman, 1993). The nutrients phosphorus (P) and nitrogen (N) are the primary nutrient-limiting elements for rich fens (Verhoeven and Schmitz, 1991; Koerselman and Meuleman, 1996; Boeye et al., 1997; Wassen et al., 2005; Cusell et al., 2014b). Since nutrient availability is determined both by the balance of nutrient in- and outputs and by
the internal cycle within the ecosystem, generally a distinction is made between external and internal eutrophication.

External eutrophication is defined as the increase of nutrient availability as a result of input from outside of the fen system. Influx of nutrient-rich surface water and groundwater, together with the major input of mainly N via atmospheric deposition, has caused severe deterioration of fens in the Netherlands over the past decades (Koerselman et al., 1990; Koerselman and Verhoeven, 1992; Lamers et al., 2002; 2015).

The increase of nutrient availability as a result of enhanced mobilization from the soil itself is called internal eutrophication (Roelofs, 1991; Smolders et al., 2006). Microbial mineralization of organic N and P is a major source of nutrients (Chapin, 1980; Verhoeven, 1986; Verhoeven et al., 1988). Particularly upon increased oxygen availability, and hence stimulation of decomposition rates, large amounts of nutrients can be released by means of mineralization of peat soils (Williams and Wheatley, 1988; Bridgham et al., 1998; Updegraff et al., 1995; Olde Venterink et al., 2002). In addition, P-availability may increase under anaerobic conditions as a result of net P-mobilization due to Fe reduction (Patrick and Khalid, 1974). Especially in Fe-rich soils with high P-contents, this anaerobic P-mobilization can be severe (Loeb et al., 2008; Zak et al., 2010; Cusell et al., 2013a). These ways of nutrient legacy from the topsoil can pose a major constraint on the restoration of fens, especially in (former) agricultural areas (Lamers et al., 2002; Zak et al., 2010).

Toxicity
Especially in agricultural areas, toxicity may be an additional problem for the rehabilitation of rich fens. As a result of fertilization and reduction of nitrate, but also as a result of atmospheric N-deposition (Verhoeven et al., 2011), ammonium concentrations may strongly increase, potentially reaching toxic concentrations to brown mosses such as *S. scorpioides* (Paulissen et al., 2004). In addition, sulfide and Fe(II) are considered potential toxins to rich fen vegetation (Lamers et al., 2015).

1.3. Restoration

Restoration objectives
Rich fen management aims at both the rejuvenation of rich fens via hydrosere succession from aquatic vegetation in open water, and the inhibition or resetting of the transition from present rich fens to poor fens or bogs.

The absence of hydrosere succession, and hence the absence of newly formed rich fens is generally attributed to P-eutrophication of surface water and banks of turbaries (Lamers et al., 2002), toxicity of sulfide and/or ammonium in underwater
soil pore water (Roelofs, 1991; Smolders and Roelofs, 1993; Lamers et al., 2013), and the absence of species facilitating terrestrialization by habitat and/or dispersal constraints (Lamers et al., 2015). Both via external P-inputs and internal P-mobilization, growth of highly productive phytoplankton is stimulated, resulting in turbid surface waters and decline of macrophytes (Scheffer et al., 1993). Although the water quality in Dutch wetlands has slightly improved over the past 15-25 years, new development of rich fens with *S. scorpioides* is yet absent.

Moreover, active management of rich fens is focused on preventing transition to *Sphagnum*-dominated poor fens or bogs (Van Diggelen et al., 1996; Lamers et al., 2002). Without active management, only acid fens and bogs/woodlands will remain. So, succession in rich fens needs to be slowed down or even inhibited, especially given the fact that new formation is hardly taking place. Annual mowing is necessary, as highly competitive, fast-growing plant species easily become dominant at the expense of lower, slow-growing species, especially under more eutrophic conditions. Further, nutrients can be removed from the system by harvesting, leading to increased species-richness (Vermeer and Berendse, 1983). Moreover, it is essential that the top of the peat layer stays in direct contact with minerotrophic, base-rich and nutrient-poor ground or surface water to keep favorable conditions for minerotrophic plant species and brown mosses, and to prevent favorable conditions for *Sphagnum* spp.

**Water table fluctuations as a restoration measure?**

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. In pristine wetlands, however, water levels vary with the meteoric and groundwater balances in and around these wetlands (Baker et al., 2009). From a management perspective, the re-establishment of fluctuating water levels is considered for non-pristine fens in order to optimize the generic ecological quality (Vermeer and Joosten, 1992; Lamers et al., 2002; Cusell et al., 2013b). Since fluctuation of the water level is a major factor determining biogeochemical and ecohydrological processes and functioning of wetlands, potential benefits and disadvantages of re-establishment of fluctuating water tables have been considered in previous studies (e.g. Mettrop et al., 2012; Cusell et al., 2013b; 2014a).

During periods with lower water levels, aerobic oxidation processes prevail due to oxygen intrusion into the soil, potentially decreasing the ANC and pH (Stumm and Morgan, 1996), and increasing nutrient-mineralization (Olde Venterink et al., 2002). These effects could hamper the development of protected brown moss vegetation in rich fens, especially during summer (Cusell et al., 2013a). However, temporary drought may be beneficial to some extent, since Fe-oxidation can lead to rapid binding of phosphate in the soil (Richardson, 1985), which may temporar-
ily reduce P-availability in porewater that may be important to conserve P-limited vegetation types. Moreover, the impact of drought may strongly differ among fens with different biogeochemical characteristics and vegetation. In fens with high iron (Fe) and/or sulfur (S) contents, the effects of drought-induced oxidation and acidification may be stronger than in calcium (Ca) rich fens, because Ca and CaCO$_3$ are not redox sensitive and changes in pH can be buffered (Stumm and Morgan, 1996). The response of P-availability to drought may also differ among fen types, since the P-binding capacity of the soil under oxic conditions is expected to strongly depend on the soil Ca and/or Fe contents. In addition, a high drought incidence can 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). All these combined effects of a higher drought incidence may lead to favorable conditions for $Sphagnum$ spp. at the expense of protected rich fen brown mosses.

During periods with increased water levels, inundation may occur. In the case of water rich in Ca and HCO$_3$, inundation can potentially increase soil ANC via infiltration, and also by internal alkalinity generation as a result of reduction processes (Stumm and Morgan, 1996). At the same time, however, 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 anaerobic P-mobilization can be severe (Loeb et al., 2008; Zak et al., 2010; Cusell et al., 2013a). Moreover, high sulfate reduction rates and formation of iron sulfides may result in reduced soil P-binding to Fe, and hence additional P-mobilization in S-rich soils (Caraco et al., 1989; Smolders and Roelofs, 1993; Lamers et al., 1998). In addition, anaerobic conditions may lead to the formation of potential phytotoxins such as ammonium, sulfide, and Fe(II) (Lamers et al., 2015). Increased surface water influence, as a result of inundation, can also lead to higher nutrient inputs (external eutrophication; e.g. Wassen et al., 1996). In relatively nutrient-poor (mesotrophic) fens adjacent to agricultural areas, external P-input can be highly detrimental (Koerselman and Verhoeven, 1992; Lamers et al., 2015). This effect may also strongly depend on biogeochemical characteristics of the peat soil.

1.4. Main objectives and thesis outline

The main question raised in this thesis is: what are the ecological benefits and drawbacks of re-establishment of water level fluctuations as a management tool in rich fens, and what can be concluded after weighing these benefits and drawbacks in terms of nature and water management? The sequence of chapters is based on an increasing scale in experimental setup. In Chapter 2, the effects of different gradations
of drought on acidification and mineralization rates are studied in a long-term incubation experiment, involving peat soil samples from brown moss-dominated rich fens and Sphagnum-fens. To gain more detailed insight into the influence of vegetation development during water level manipulations with different water qualities, and the importance of chemical soil characteristics, Chapter 3 describes a mesocosm experiment in which subsequent periods of drought and inundation were simulated with P-poor and P-rich supply-water. Chapter 4 and 5 report on large-scale field experiments, assessing the biogeochemical impacts of 2 weeks of inundation both in summer and winter, and 2 weeks of drought in summer. Both floating and non-floating fens are included with different fen vegetation types. In Chapter 6, the relative importance of Ca and Fe for nutrient availability, plant productivity and species composition in brown moss-dominated rich fens is discussed, based on extensive analyses of soil samples from the Netherlands (strong anthropogenic forcing) and central Sweden (weak anthropogenic forcing). Finally, Chapter 7 provides a synthesis in which results and conclusions from the preceding chapters are discussed and integrated in a comparative overview of potential ecological benefits and drawbacks from a management perspective.

References


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General introduction

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