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Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach

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ABSTRACT

Fens represent a large array of ecosystem services, including the highest biodiversity found among wetlands, hydrological services, water purification and carbon sequestration. Land-use change and drainage has severely damaged or annihilated these services in many parts of North America and Europe; restoration plans are urgently needed at the landscape level. We review the major constraints on the restoration of rich fens and fen water bodies in agricultural areas in Europe and disturbed landscapes in North America: (i) habitat quality problems: drought, eutrophication, acidification, and toxicity, and (ii) recolonization problems: species pools, ecosystem fragmentation and connectivity, genetic variability, and invasive species; and here provide possible solutions. We discuss both positive and negative consequences of restoration measures, and their causes. The restoration of wetland ecosystem functioning and services has, for a long time, been based on a trial-and-error approach. By presenting research and practice on the restoration of rich fen ecosystems within agricultural areas, we demonstrate the importance of biogeochemical and ecological knowledge at different spatial scales for the management and restoration of biodiversity, water quality, carbon sequestration and other ecosystem services, especially in a changing climate. We define target processes that enable scientists, nature managers, water managers and policy makers to choose between different measures and to predict restoration prospects for different types of deteriorated fens and their starting conditions.

Key words: agriculture, carbon sequestration, climate change, eutrophication, ecosystem services, hydrology, nature management, peatland, wetland.

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I. INTRODUCTION

(1) General introduction

This review focuses on the restoration of rich fens in Europe and North America, and includes their vegetation succession, e.g. changes as a result of paludification of drained areas, the hydrosere towards fens by the encroachment of open water by vegetation, and the transition to poor fens and bogs by the gradual loss of contact with minerotrophic water. We feel that it is essential to include the succession from shallow surface waters to floating rich fens, as this process of terrestrialization has become a major challenge in many degraded fen landscapes in Europe (Lamers, Smolders & Roelofs, 2002*b*). After a description of important ecosystem processes in these systems, the major effects of land-use change will be explained. This hydrological, biogeochemical and ecological knowledge will be used to define restoration measures based on types of fen alteration and starting conditions, and to indicate challenges and opportunities for the hydrological

restoration of drained fens, the transition of surface water bodies to rich fens, and the retransformation of agricultural lands to fens, which is the main restoration trajectory in Europe. In North America, post-industrial landscape (after horticultural peat extraction or oil-sand extraction) will rely on a drier 'paludification' approach, aiming at the restoration of a waterlogged top layer.

Many restoration efforts to date have been based on trial and error, with variable levels of success. Based on disturbance type and initial conditions, we point out how to determine restoration opportunities and targets (ecosystem services including biodiversity), and to apply measures using an evidence-based approach.

(2) Fens and fen landscapes

(a) *Hydrogeomorphology*

The formation of peat (i.e. soil containing >30% organic matter on a dry mass basis) takes place when decomposition

rates are lower than primary production, as a result of the low availability of oxygen due to waterlogged or flooded conditions. In total, about 4 million km² of the earth is covered with peatland (>30 cm peat); this is about 3% of the land surface and >30% of global soil C, representing a stock of 400–550 Pg (gigaton) C. It is estimated that an additional 5–10 million km² of peatland is present with a peat layer less than 30 cm thick, mainly in permafrost areas (Parish *et al.*, 2008). Peatlands contain 10% of the earth's fresh-water volume, and therefore play a significant role in global hydrology (Gorham, 1995; Joosten & Clarke, 2002). About 80% of the area of all peatlands is found in continental (85% boreal) and temperate regions of the northern hemisphere, half of which is in North America (Gorham, 1995; Joosten & Clarke, 2002). Canada contains the largest area, 1.24 million km² of peatland representing a stock of 154 Pg C (Roulet, 2000), and the USA has 0.61 million km² of peatland, mainly in Alaska (Joosten & Clarke, 2002; Strack, 2008). In Europe, an area of 0.51 million km² is covered by peatlands, of which 0.24 million km² is in the Russian part of Europe, and 0.17 million km² in Finland and Sweden (Joosten & Clarke, 2002). The peatland area used for agriculture is estimated at 15% for Canada, 10% for the USA, and varies enormously among European countries, from low values of 2% for Finland and 5% for Sweden, to 85% for Germany and the Netherlands (Strack, 2008). The areas that have been drained for forestry are, however, much larger: e.g. almost 55% of the peatland area in Finland (Turunen, 2008).

To facilitate wet conditions in peatlands, the influx of water (deposition, surface water, groundwater) has to be large enough to compensate for losses due to outflow, runoff, recharge and evapotranspiration. As this hydrological balance is controlled by both influx and efflux, a change in either can lead to increased drainage, changed hydroperiods, or increased flooding. Rich fens may be defined as ecosystems with slightly acidic to circumneutral peat as a result of sufficient pH buffering. This is generally the result of the influx of a substantial amount of mineral-rich water from surface water inflow and/or groundwater discharge, or (especially for thinner peat layers) largely depending on the buffering conditions of the subsoil (minerotrophic peatland, geogenous peatland; Gore, 1983; Bridgham *et al.*, 1996; Wheeler & Proctor, 2000; Joosten & Clarke, 2002; Bedford & Godwin, 2003; Bonn *et al.*, in press), in contrast to ombrotrophic peatlands (bogs) that are mainly or exclusively fed by rainwater. However, because of the myriad of different geohydrological settings for fens and bogs, Bridgham *et al.* (1996) suggested to define these terms broadly, only based on geochemistry and dominant plant species rather than ontogeny, geohydrology, nutrient availability, or the presence or absence of non-dominant 'indicator' plant species. Because of the gradients between different types, and differences in terminology, it is difficult to provide a number for the percentage of peatlands globally that may be classified as fens. It has been estimated that fens cover 26% of the global wetland area, and 42% of the global

peatland area, representing about 1.5 million km² and a stock of around 200 Pg C (Joosten & Clarke, 2002; Ramsar Convention Secretariat, 2013). For Canada, fens comprise 34% of all peatlands (0.4 million km²; Tarnocai, Kettles & Lacelle, 2000). For Europe, the contribution of fens to the total area of peatlands varies widely, from 1% in the UK due to the large areas of blanket bogs (JNCC, 2011) to 48% for Russia (Minayeva, Sirin & Bragg, 2009), and an average of 78% for Central Europe (Bragg & Lindsay, 2003). Based on the available figures for total peatland cover (Roulet, 2000; Joosten & Clarke, 2002), we estimate that North America has 0.5–0.8 million km² of fens. Given the fact that the European part of Russia, Scandinavia and Central Europe contains the majority of peatlands in Europe, we estimate that fens cover 0.2–0.3 million km² in Europe. For an extensive description of different mire types including bogs and marshes, we refer readers to other publications (Moore & Bellamy, 1974; Bridgham *et al.*, 1996; Joosten & Clarke, 2002; Mitsch & Gosselink, 2007).

Fens include a wide variety of ecosystem types, including peat-forming systems such as poor fens, rich fens, fen woodlands (carr woods in Europe; swamps in America), and wet prairies on peat soils. In addition, there are fen meadows and prairies on degrading peat soils, shallow ponds, lakes, and marshes and prairies on mineral soils where there is little peat formation. Open water bodies are both naturally present as lakes, oxbow lakes and pools in river valleys and other landscapes with depressions, and man-made in turbaries (peat extraction pits) and oil-sand pits. Fen peat is formed by the accumulation of dead organic matter of mainly graminoid plants (families Cyperaceae, Poaceae, Juncaceae) and a great range of aquatic macrophytes in shallow water bodies in river or stream valleys with a slow, unidirectional flow of mineral-rich water (e.g. Everglades, USA; Biebrza, Poland), or in lakes, pools or other landscape depressions receiving a slow flow of discharging groundwater and/or surface water (e.g. rich fens in New York state, USA, Norfolk Broads, UK, Weerribben-Wieden, The Netherlands). The groundwater flows in fens with discharge may be regional or more local, and the underlying material can be sand, clay, chalk or rock, as long as the water balance, pH-buffering minerals (including bicarbonate) and nutrients enable graminoid growth and accumulation of peat under anaerobic, minerotrophic conditions. By the accumulation of peat, fens show a long-term succession towards vegetation types that develop under less buffered and more nutrient-poor conditions (poor fens, bogs). As a result, they often occur in large peatland complexes showing fen–bog gradients and mosaics related to heterogeneity in hydrology, buffering capacity, nutrient supply and peat accumulation. Although the water level has to be high for long enough to ensure peat accumulation, it can still show large variations from no fluctuation to fluctuations between –50 cm (50 cm below surface level; summer) and > 1 m (winter), affecting both vegetation and peat accumulation. As a result, their hydrogeomorphology shows large variation, which is important

to consider with respect to restoration targets and options in degraded fens.

(b) Plant growth and pH

Depending on the type of litter produced, nutrient availability and acid-neutralizing capacity (ANC), the peat may be highly decomposed, lacking structure and with a black colour (high ANC, high nutrient levels, readily decomposable plants) or more structured with recognizable peat-forming plants including sedges, reeds and mosses. Depending on their ANC, fens may be divided into rich fens (higher ANC) or poor fens. The pH in wet rich fen peat (including floating fens) and the soils of shallow fen surface waters is determined by the bicarbonate–carbon dioxide (HCO_3^- – CO_2) buffering system, with pH typically around 6–6.5 and higher rates of decomposition as compared to acidic peatlands (Lamers *et al.*, 2002b). In shallow waters, the supply of CO_2 from either decomposition of peat (soil respiration) or groundwater partly compensates for its outgassing and photosynthetic uptake by aquatic plants and algae. This enables the occurrence of non- HCO_3^- -using submerged plant species such as *Hottonia palustris* L.

Rich fens are generally more species-rich than poor fens and bogs and characterized by graminoid species including Cyperaceae, but can also include a large proportion of dicots and brown mosses. Mineralization rates and nutrient availability are not necessarily higher in fen plant communities than in bog plant communities. The uptake of nutrients, rather than their availability, appears to form the principal constraint for plant growth in peatlands (Waughman, 1980; Verhoeven, Maltby & Schmitz, 1990; Bridgham *et al.*, 1996; Koerselman & Meuleman, 1996; Aerts, Verhoeven & Whigham, 1999; Kooijman & Hedenäs, 2009). The term ‘minerotrophic’ strictly refers to the higher concentrations of base cations [of calcium (Ca), magnesium (Mg), sodium (Na) and potassium (K)] whereas ‘eutrophic’ refers to the higher availability of primary nutrients [in particular phosphorus (P), nitrogen (N), and potassium (K)].

If peat growth exceeds the minerotrophic water layer, supply of HCO_3^- and cations decreases and buffering of the incoming rainwater becomes less effective (Lamers *et al.*, 2002b). In addition, aerobic oxidation processes in the peat generate acids, the environment becomes less favourable for minerotrophic plants, and acidophilic *Sphagnum* species become dominant. Due to acid production by *Sphagnum* spp. (mostly organic acids from its decomposition, but also by cation exchange), ANC declines further. Deposition of acidifying reactive sulfur (S) and nitrogen compounds may speed up this process, but the transition is largely due to natural succession. Once bicarbonate has been consumed to a large extent, the exchange of base cations from binding sites in the peat becomes the main buffering mechanism (Lamers, Van Roozendaal & Roelofs, 1998b). This second buffering system is very important for fen plants if the top layer dries out when water tables drop due to natural fluctuation or anthropogenic desiccation.

(c) Carbon sequestration

Fast peat formation is a matter of high biomass production rates and low decomposition rates. Even though above-ground net primary production (NPP) rates in fens dominated by vascular plants may range between 25 and $1500 \text{ g m}^{-2} \text{ year}^{-1}$, values often exceed $1000 \text{ g m}^{-2} \text{ year}^{-1}$ (Bartsch & Moore, 1985; Saarinen, 1996; Vitt *et al.*, 2009). As root production significantly contributes to C sequestration, this is an important component. Vitt *et al.* (2009) estimate NPP values of $150\text{--}200 \text{ g m}^{-2} \text{ year}^{-1}$ for moss layers in fens, $300\text{--}350 \text{ g m}^{-2} \text{ year}^{-1}$ for above-ground biomass of vascular plants, and about $500 \text{ g m}^{-2} \text{ year}^{-1}$ for their below-ground biomass. Data about below-ground production rates in fens are, however, scarce and total production rates of fen vegetation may therefore be much higher than the total values presented in literature. For *Sphagnum*-dominated mires (bogs and poor fens), in comparison, NPP ranges are generally lower and range between 120 and $1000 \text{ g m}^{-2} \text{ year}^{-1}$, of which *Sphagnum* spp. contribute $20\text{--}380 \text{ g m}^{-2} \text{ year}^{-1}$ (Moore *et al.*, 2002).

Vascular plants such as *Menyanthes trifoliata* L. and *Carex* spp. decompose much faster than *Sphagnum* spp. (65–80% mass loss in 3 years compared to 15%; Moore, 1989; Graf & Rochefort, 2009). Although species may form a range from peat-forming to non-peat-forming species depending on their decomposability, other factors such as nutrient composition, water quality, water level and temperature all have a strong impact on decomposition rates. Site conditions, including water table, temperature and nutrient availability, can be more important than the chemical composition of the plant material (Rejmánková & Houdková, 2006; Moore, Bubier & Bledzki, 2007; Sarneel *et al.*, 2010). This may partly explain the inter-annual variability and the large ranges of C sequestration found for similar vegetation types. The net ecosystem exchange (NEE) of intact fens ranges between -5 and $-40 \text{ g C m}^{-2} \text{ year}^{-1}$ (C sink), which is lower than the range for bogs (-3 to $-160 \text{ g C m}^{-2} \text{ year}^{-1}$; Byrne *et al.*, 2004; Limpens *et al.*, 2008; Wieder *et al.*, 2009). The fact that fens show a similar or lower C sequestration compared to bogs, even though production rates can be much higher, can be explained by their higher decomposition rates.

II. MAJOR LAND-USE CHANGES

(1) Drainage, fertilization and peat extraction

It has been estimated that half of the global wetland area (almost entirely freshwater wetlands) has been lost due to human activities (Zedler & Kercher, 2005). The remainder is heavily degraded. In northern countries, most of the changes took place during the first half of the 20th Century (Joosten & Clarke, 2002). In countries with rapidly developing economies, in particular, the rate of wetland loss is accelerating. Half of this loss is due to drainage for

agricultural use (Europe 56%, North America 65%; Joosten & Clarke, 2002). For the conversion to agricultural lands, all types of fens have been used with variable intensities of dehydration, tillage and fertilization, leading to biodiversity loss. In the USA, states that show large-scale agricultural land use (California, Iowa, Illinois, Missouri, Ohio, Indiana) have lost more than 80% of their wetlands including fens (Bedford & Godwin, 2003; Zedler, 2004). In European countries, a large proportion of former fens have been converted to agricultural use (Grootjans & Van Diggelen, 1995; Joosten & Clarke, 2002; Grootjans *et al.*, 2006; Holden, Gascoign & Bosanko, 2007). Also in many other areas, such as the Mesopotamian Plain in Iraq, large areas of wetland have been drained (Richardson & Hussain, 2006).

Many peatlands worldwide have been drained and converted into highly productive agricultural areas, in which the peat layer is rapidly declining. The % C in fen peat equals that of bogs, amounting to 45–55%, and bulk densities around 100 g dry mass dm⁻³. In contrast to bogs, fens often show higher nutrient availability and are therefore more suitable for the production of cash crops, although many have been heavily fertilized to increase production rates (Galloway *et al.*, 2004). In addition, fen peat layers can be exposed after oil-sand extraction (Graf, Bérubé & Rochefort, 2012; Vitt & Bhatti, 2012), or when peat has been extracted down to fen-peat layers by horticultural industries (Rochefort, *in press*). In European countries both bogs and fens were exploited for fuel, leaving large abandoned industrial cutaway peatlands. Although fen turf had a higher efficiency in producing heat, bogs were generally easier to drain.

In highly populated areas of Europe, fen remnants generally cover areas that were difficult to drain. Some of these remaining fens were used for hay production (fen meadows) or cattle grazing during drier periods. As a result of above-ground biomass removal, slow-growing species could compete with fast-growing species, increasing biodiversity. In the UK, Germany and the Netherlands, this historical land use of hay making has even been incorporated in nature management to conserve or redevelop endangered wetland types that harbour high biodiversity (fen meadows and floating fens; Van Wirdum, Den Held & Schmitz, 1992; Wheeler & Shaw, 1995). Biomass removal is particularly important for the biodiversity of more eutrophic fens, as highly competitive, fast-growing species easily become dominant in the absence of mowing as a result of partial drainage and/or high nitrogen deposition rates.

The extraction of peat not only lowered water table levels to facilitate mining, but also led to new aquatic habitats. Due to storms smaller turbaries changed into lakes (e.g Norfolk Broads, UK; Wieden-Weerribben, The Netherlands). Likewise, the construction of oil-sand extraction pads in fens in North America creates approximately 1 ha ponds once the pad has been abandoned. The pad is usually constructed in winter when frozen ground facilitates access. Trees are cut and a layer of 1.5–2 m of mineral material is charged on top of geotextile material to create a stable platform. At the

end of oil-pumping activity, the pad is retrieved (in winter), leaving a relatively large depression.

(2) Peat loss and land subsidence

Fens that have been drained and transformed into agricultural fields no longer function as net sinks for atmospheric C (a key ecosystem service), but function as a net C source to the atmosphere (Pfadenhauer & Klötzli, 1996; Kasimir-Klmedtsson *et al.*, 1997), with additional losses of C to surface waters and groundwater. It has for instance been estimated that 4 m of peat have been lost from Holme Fen, UK, since 1851 due to drainage and oxidation of the peat. Higher temperatures, changes in precipitation and higher rates of evapotranspiration as a result of climate change, and irreversible physical changes to the peat may increase desiccation events and concomitant C-loss (Evans, Burt & Adamson, 1999; Estop-Aragones & Blodau, 2012). Increased decomposition rates and soil settlement have led to severe land subsidence, necessitating additional hydrological measures to keep arable lands dry. In coastal areas, land subsidence leads to severe safety issues (flooding risks), especially in relation to sea-level rise as a result of climatic change. To ensure agricultural use of fen areas, more advanced water works became necessary, including a dense network of pumping stations, levees, canals, ditches and trenches. In the Netherlands, subsidence even led to the remarkable situation whereby the surface water level in many canals is now considerably higher than the soil surface in the adjacent fen polders.

(3) Changes in ecosystem services

Most fens in agricultural landscapes have lost the majority of their original ecosystem services (Table 1; Richardson, 1994; De Groot, Wilson & Boumans, 2002; Bedford & Godwin, 2003; Zedler & Kercher, 2005; Smith *et al.*, 2008; Verhoeven & Setter, 2010) replacing their original service with cropland or urban development. At a global scale, 16% of the former peatland area has been lost due to anthropogenic activity. For North America this is 5%, and in Europe more than half (52%) has been lost (Joosten & Clarke, 2002). Once multi-functional wetlands showing a high biodiversity, they have become mono-functional arable lands or meadows with very high water use (Foley *et al.*, 2005). The Everglades National Park, for instance, comprises only 54% of the original Everglades (Richardson, 2010). Fens that used to serve as peat-forming systems that sequester carbon, now show carbon losses and land subsidence. In this way, fens have also lost their service as a supplier of fuel and horticultural substrate, although peat extraction is, ecologically, a very questionable service and highly undesirable in intact peatlands. The converted fens have also lost their regulating service in water storage and hydrological buffering at the landscape scale, which is even more severe given current climate change. Water quality has become poor, and instead of nutrient sinks (water purification), eutrophicated fen areas have become sources

Table 1. An overview of fen ecosystem services, and their modifications as a result of land-use change

Original services	Modifications
Provisioning services	
Natural area	Agricultural area, urban area
Freshwater supply	Loss of water, bad water quality
Food (including fish, waterfowl) production	Crop production
Crafts and building supplies (reed, rushes)	Loss of this material
Peat for fuel, horticulture, pollutant sorption, medication (sorberent)	Peat removed, no new production
Supporting services	
Biodiversity (landscape, ecosystem, and species scale)	Biodiversity loss at all scales
Peat soil formation	Peat loss, land loss, land subsidence
Peatland biogeochemistry	Strongly altered biogeochemical cycling of elements and water
Regulating services	
Surface water and groundwater regulation (also water retention and storage with respect to climate change)	Hydrological disturbances, water losses, desiccation, acidification
Nutrient sink and water purification	Nutrient source, no purification
Carbon sink for atmospheric CO ₂	Carbon source
Flood protection	Increased flooding risks due to loss of wetland buffer, land subsidence, land loss
Cultural services	
Recreation in nature (also provisioning health)	Loss of recreational and health value
Mosaic, cultural-historic landscape	Uniformity, loss of cultural-historic values
Nature and environmental education	Education about peatland degradation
Archaeological and palaeontological record in peat	Loss of this record
Inspirational values (cultural communities, art, etc.)	Loss of these values

of nutrients. Biodiversity has greatly decreased, both at the species level and at the ecosystem and landscape level. In addition, the protective role of peatlands with respect to flooding has vanished in many areas, especially where land accretion has changed to subsidence. As a result of the change in land use, recreational and educational values have also decreased.

III. HABITAT AND ECOSYSTEM CONSEQUENCES

(1) Drought

The agricultural use of peatlands in Europe generally involves severe hydrological changes at the landscape scale. Therefore, both the deterioration and the rehabilitation of fens should not only be considered at the local scale, but also on a larger scale, integrating terrestrial and wetland systems (Zedler, 2000; Brown, Mitchell & Beresford, 2004). The direct result of water table drawdown is the loss of wet and moist habitats for both fauna and flora, such that vegetation favored by drier conditions replaces wetland plant communities. The intrusion of oxygen stimulates peat decomposition and C loss to the atmosphere, as oxygen stimulates the oxidation of phenolic compounds that are a major constraint for overall decomposition rates, rather than only serving as a general preferred electron acceptor. As a result, the microbial community is able to grow, leading to positive feedback on decomposition rates (Freeman, Lock &

Reynolds, 1993; Freeman, Ostle & Kang, 2001*b*; Fenner & Freeman, 2011). The extent of the drought response strongly depends on the type of peat (Mettrop *et al.*, 2014). In addition to C loss to the atmosphere, the losses of dissolved and particulate organic carbon increase (Freeman *et al.*, 2001*a*).

Depending on actual nutrient concentrations, increased mineralization of P, N, K and other nutrients could result. The increase in decomposition and nutrient mineralization rates due to drainage (Fig. 1) may differ as a result of the extent of desiccation, vegetation composition, and peat structure and composition (Schlesinger & Andrews, 2000). As drought has severe effects on vegetation composition and litter quality is a major driver of decomposition rates, there is a strong indirect effect on C loss to the atmosphere (Strakova *et al.*, 2011; Vile *et al.*, 2011).

(2) Acidification

Acidification is a natural process in fens as a result of peat accumulation, leading to the progressive isolation of the top layer from bicarbonate and mineral supply. In addition to this biogeochemical acidification, vegetation changes leading to domination of *Sphagnum* spp. instead of brown mosses such as *Scorpidium scorpioides* (Hedw.) Limpr. and *Hamatocaulis vernicosus* (Mitt.) Hedenäs, may add to the acidification of rich fens. High P influxes can accelerate this succession due to excessive growth of the relatively alkalinity-tolerant species *Sphagnum squarrosum* Crome (Kooijman & Bakker, 1995; Kooijman & Paulissen, 2006). Although the transition of minerotrophic to ombrotrophic species on floating fens is largely due to natural succession, active management

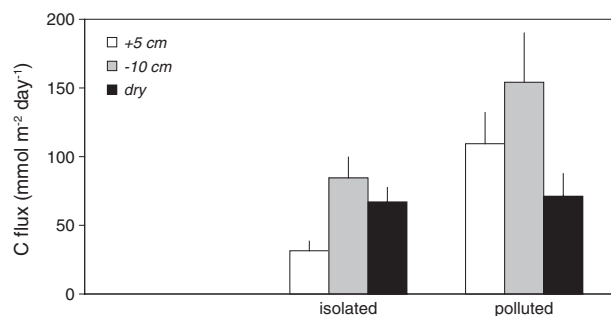


Fig. 1. Total carbon fluxes to the atmosphere from fen peat monoliths after 10 weeks of either flooding (+5 cm), lowering of the water table 10 cm below the soil surface (−10 cm), and left to dry out. Polluted: peat polluted by P and S from agriculture; isolated: same peat deposits but isolated from agricultural influence. Note that C loss from flooded polluted peat equals C loss from drained (−10 cm) unpolluted peat. 100 mmol C m⁻² day⁻¹ equals 1.2 g C m⁻² day⁻¹. After Lamers (2001). Values are means + S.E.M. ($N = 5$).

in Europe is often aimed at the earlier minerotrophic vegetation, by sod-cutting, digging additional channels or applying lime, with highly variable outcomes. The rationale for this type of management (fixation of successional phase) is that this vegetation type including many threatened species would be preserved, as new formation of this fen type is scarcely occurring at present (Beltman *et al.*, 1996; Van Diggelen, Molenaar & Kooijman, 1996; Lamers *et al.*, 2002b; Cusell *et al.*, 2013).

In addition to this natural acidification, drainage of fens will often lead to acidification. Desiccation of peat always leads to the production of H⁺ due to aerobic oxidation reactions including nitrification, iron oxidation and sulfur oxidation (Lamers *et al.*, 1998b). Whether or not pH decreases will depend on the ANC of the peat. To avoid acid conditions, farmers apply lime to drained peatlands to ensure that their crops do not suffer from adverse pH, and to increase nutrient availability by the stimulation of mineralization. A low pH in the rhizosphere has important consequences for rich fen plant species both in terms of direct and indirect effects of H⁺ toxicity. At pH levels below 5–6, H⁺ is exchanged for base cations at exchange sites in the peat. The level of base saturation will therefore decrease with acidification and the availability of Ca and Mg will decrease as a result of leaching. Therefore, the level of base saturation is an important peat characteristic with respect to acidification. If acidification is stronger, pH may drop below 4.5 and aluminium (Al) and iron (Fe) will dissolve. In addition, lowering of the pH may decrease nitrification rates in the top layer, leading to the accumulation of ammonium. For a number of species growing in riparian litter fens (*Junco - Molinion*) that have lower water tables in summer, both ammonium toxicity and Al toxicity have been shown during acidification (De Graaf *et al.*, 1997; Paulissen *et al.*, 2004; Van den Berg *et al.*, 2005). Peats rich in Fe (as a result of actual or former groundwater discharge) also show stronger acidification as a result of desiccation. In valley fens, meadows that had not been limed

had become strongly acidified as a result of desiccation (Grootjans *et al.*, 1988). Because of oxygen intrusion, rates of N mineralization and P immobilization by Fe³⁺ compounds had both become higher, which led to the dominance of dryland graminoid species.

Increased airborne N and S inputs may strongly exacerbate acidification due to direct influx of nitric acid and sulfuric acid, but also indirectly (Gorham, Bayley & Schindler, 1984). Although ANC in rich fen peat is relatively high, pH has still been shown to have decreased slightly in Scandinavia, and decreased significantly in many other parts of Europe (Gunnarson, Rydin & Sjörs, 2000; Kooijman, 2012). Sulfide and ammonium accumulated in the peat will become oxidized during periods with lower water tables, generating acid.

(3) Eutrophication

Eutrophication is defined as the increased availability of elements limiting primary production (Von Liebig, 1843; Einsele & Vetter, 1938). Mainly in the second half of the 20th Century, many agricultural areas and adjacent less-disturbed areas became eutrophic or hypertrophic. Due to direct application of fertilizer and manure, the input of both N and P has strongly increased in drained peatlands (Verhoeven, Koerselman & Meuleman, 1996; Matson *et al.*, 1997; Verhoeven *et al.*, 2006). In European peatlands, plant-available P (Olsen *et al.*, 1954) has increased from 250–500 μmol l⁻¹ peat in unfertilized areas to values of 1000–10000 μmol l⁻¹ in fertilized peatlands (Lamers *et al.*, 2006; A. J. P. Smolders & L. P. M. Lamers, unpublished results). In addition, eutrophication has been caused by influx of nutrient-rich surface water or groundwater, and increased atmospheric deposition of nutrients (mainly N). A large amount of the N applied as fertilizer evaporates as ammonia (NH₃) or is washed out as nitrate (NO₃⁻) or ammonium (NH₄⁺) to the surface water and groundwater. Especially in peat soils, P is much less mobile and accumulates in the top layers, mainly bound to the amorphous Fe and Al fractions (Richardson, 1985) but also in Ca fractions (Boyer & Wheeler, 1989). This nutrient legacy in the topsoil poses a major constraint on the restoration of fens at former agricultural sites (Lamers *et al.*, 2002b; Van Dijk *et al.*, 2007; Smolders *et al.*, 2008; Zak *et al.*, 2010). The loss of P is largely *via* surface runoff, erosion and loss of organically bound P.

The input of airborne N is an important anthropogenic source for N in agricultural areas, caused mainly by agricultural ammonia emissions and by the emission of nitrogen oxides during combustion processes (traffic and power plants; Bobbink, Hornung & Roelofs, 1998). As a result, bulk deposition rates can be as high as 40 kg N ha⁻¹ year⁻¹, or even higher, far exceeding the estimated background level of 0.5–1 kg N ha⁻¹ year⁻¹. This means that even after the cessation of active fertilization or inputs from polluted groundwater or surface water, fens may still receive high N inputs (Koerselman, Bakker & Blom, 1990).

(4) Internal eutrophication

Next to eutrophication by increased inputs, internal nutrient cycling may also be accelerated by changes in water level and water quality. This process has been termed internal eutrophication (Roelofs, 1991; Smolders *et al.*, 2006). As explained in Section II.1, drainage will lead to stimulation of decomposition rates, not only leading to C loss as CO₂ and dissolved organic carbon (DOC), but also to increased mineralization of nutrients. This accumulation of nutrients per unit volume (which is the relevant unit of measure from a plant's perspective) as a result of drought is further enhanced by the increase in bulk density due to C loss and peat compaction.

Internal eutrophication may, however, also occur under anaerobic conditions. Increased surface water sulfate input has, for instance, been shown to promote eutrophication in fens in the Netherlands, Germany, and USA, and also enhance the production and bioaccumulation of toxic methylmercury (Branfireun, Heyes & Roulet, 1996; Lamers *et al.*, 2002b; Smolders *et al.*, 2010; Orem *et al.*, 2011). Sulfate will serve as an alternative terminal electron acceptor (given the low availability of oxygen), speeding up overall decomposition (Fig. 1; Vile *et al.*, 2003). Increased inputs of SO₄²⁻ may additionally mobilize P from iron (Fe) compounds in the peat, due to its reduction to sulfide competing for iron binding sites (Caraco, Cole & Likens, 1989; Lamers, Tomassen & Roelofs, 1998a), or mobilization of P from polyphosphates by sulfur bacteria (Golterman, 2001). Whether or not sulfate-induced eutrophication occurs depends on the levels of P in the sediment and the type of binding (Lamers *et al.*, 2002b; Loeb, Lamers & Roelofs, 2008; Orem *et al.*, 2011). In the Everglades fens, a large proportion of P is bound in the Ca fraction that is not responsive to redox changes or sulfide, and P mobilization will therefore be lower than in peats showing a large proportion of Fe-bound P (Dierberg *et al.*, 2011).

(5) Vegetation responses to eutrophication

In general, increased nutrient availability leads to shifts in vegetation composition caused by competitive interactions (Grime, 1974). Strongly competitive, fast-growing species will become dominant and monopolize sunlight at the expense of others, leading to biodiversity loss (Hautier, Niklaus & Hector, 2009). However, biomass production of different species may be limited by different nutrients, suggesting that the increased availability of, for instance, N does not necessarily lead to vegetation changes. It has been shown that natural or semi-natural (i.e. mown) fen vegetation may be limited by P, N, K or even other elements. In addition, vegetation can show co-limitation, e.g. of N and P (Koerselman & Meuleman, 1996; Bedford & Godwin, 2003; Güsewell, 2004; Elser *et al.*, 2007).

Nitrogen is often the principal limiting nutrient in terrestrial and semi-terrestrial systems due to its mobility to surroundings (including losses of N₂ and N₂O to the atmosphere by microbial activity and fires) and its relatively

slow mineralization (Vitousek & Howart, 1991). However, high availability of N as a result of airborne inputs and direct fertilization can still lead to P limitation. For freshwater systems, P is generally believed to be limiting biomass production (Richardson, 1985; Hecky & Kilham, 1988; Reddy *et al.*, 1999; Schindler, 2000), although a more recent, global meta-study revealed equal importance of N and P (Elser *et al.*, 2007). Increased input of P strongly promotes the development of floating-leaved macrophytes, algae and cyanobacteria, and the growth of submerged aquatic vegetation will become limited by light. Only those species that are emergent, able to rapidly grow to the surface in spring, or possess floating leaves, will still be able to have access to sufficient light. This means that the loss of submerged vegetation in shallow surface water bodies adjacent to fens is strongly linked to P availability. As the vegetation composition and structure strongly determines faunal communities, these changes can be drastic for them. For fauna, eutrophication also generates a constraint at the landscape scale: the loss of habitat heterogeneity, which is vital for many species to be able to complete their life cycles (Verberk *et al.*, 2010; Bonn *et al.*, in press). So when we consider also the restoration of faunal communities, it is necessary to restore habitat diversity at the local and landscape scale, rather than just the rehabilitation of one particular vegetation type. For policy and nature management, information about the type of nutrient limitation is important because the different nutrients may originate from different sources, each with their own management problems. For fens, P limitation has been shown to be important to enable high biodiversity and the occurrence of rare and endangered plant species (Bedford, Walbridge & Aldous, 1999; Venterink *et al.*, 2003; Wassen *et al.*, 2005).

(6) Toxicity

An additional problem for the rehabilitation of more natural systems in agricultural areas may be caused by toxicity, both from toxins (naturally occurring substances) and toxicants (anthropogenic substances). Potential toxins include a wide range of compounds such as NH₄⁺, NH₃, H₂S, and metals such as Al (Lamers *et al.*, 2012). Sodium chloride toxicity to animals and plants can be the result of groundwater extraction or surface water use for irrigation and drinking water in coastal areas leading to salinization. In addition, storms may inundate coastal peat-extraction sites, and post-oil-sand-mining sites are saline as a result of caustic water used to extract the bitumen (Vitt & Bhatti, 2012). As most freshwater organisms are physiologically unable to cope with sodium chloride concentrations above 30–85 mmol l⁻¹ (1–3 g l⁻¹), high concentrations will seriously affect species composition (Remane, 1934; Whitfield *et al.*, 2012).

As a result of fertilization, NH₄⁺ concentrations may strongly increase in fens close to agricultural lands, both as a result of NH₄⁺ influx and as a result of dissimilatory NO₃⁻ reduction to NH₄⁺ (DNRA; Burgin & Hamilton, 2007). It has been shown that high concentration of this

N species, and especially high ammonium to nitrate ratios can be detrimental to a number of terrestrial and aquatic fen species, particularly in combination with acidification (Stevens *et al.*, 2011; Verhoeven *et al.*, 2011). In surface waters, the ammonium ion is converted to ammonia gas by increased pH (>8.5) as a result of photosynthetic activity of plants, algae and cyanobacteria. As ammonia is much more toxic than ammonium, this can pose a serious threat to fauna (including fish) and vegetation (Thurston, Russo & Vinogradov, 1981).

High loading with sulfate, as described above, can lead to accumulation of free sulfide in the peat pore water. The substance is a very strong toxin, equal to cyanide, and can have a serious negative impact on both vegetation and faunal community (Koch, Mendelssohn & McKee, 1990; Armstrong, Afreen-Zobayed & Armstrong, 1996; Smolders & Roelofs, 1996; Van der Welle *et al.*, 2006; Lamers *et al.*, 2013). For the Everglades fens, not only pollution with P from agriculture, but also sulfide toxicity may have promoted the expansion of southern cattail *Typha domingensis* Pers., an invasive species in this region (Craft, Vymazal & Richardson, 1995; Richardson, 2008).

The most important toxicants in agricultural areas are pesticides (herbicides, fungicides, insecticides, etc.) used for crop protection. The accumulation of pesticides in the food web has led to population declines of raptors and other predators including alligators, and has affected the physiology of organisms including their endocrine functioning (Solomon *et al.*, 1996; Vos *et al.*, 2000; Moorman *et al.*, 2001). Although legislation on the use of pesticides has become much more strict, and less persistent pesticides have been used in most countries since the 1960s and 1970s, concentrations can still be high in agricultural areas. Despite some progress with legislation, these scenarios continue to challenge the management of existing nature reserves in agricultural areas and complicate the conversion of agricultural land to nature.

IV. RESTORATION OF HABITAT AND ECOSYSTEM QUALITY

(1) Starting conditions and targets

Before restoring fens, targets have to be clear. It may be difficult or even impossible to restore all ecosystem services. For instance, maximizing primary production of natural vegetation to restore carbon sequestration can lead to lower plant biodiversity. We feel strongly that it is essential to choose targets based on the actual potentials, rather than on historical data, since the latter has led to many disappointments in restoration ecology. The potentials are determined by the starting conditions (type of human disturbance) and logistical options (e.g. for hydrological restoration), and different types of altered fens can be defined: Type A: excavated fens and oil sand pits; Type B: severely drained fens used as farmland; Type C: less severely drained

fens with modified hydrology; Type D: eutrophicated fen waters.

(2) Hydrological restoration

As described in Section III, fens have many of their original biogeochemical and physical properties changed, and simply rewetting areas will only lead to higher water tables and lower C emissions, which cannot be the sole ecological restoration goal. All more or less pristine fens exhibit natural variations in water table and vegetation communities are adapted to wetter and drier conditions at different times of the year (Mitsch & Gosselink, 2007). The restoration of the 'original' hydrology, i.e. before the hydrological measures carried out to convert 'badlands' into croplands, can be a great challenge. Even demonstrating the hydrological impact of a large-scale water abstraction on a wetland can be a major exercise (Whiteman *et al.*, 2004). For areas in which only minor hydrological modifications have been carried out (Type C), the blocking of drainage ditches and canals may be sufficient to achieve rewetting (Wheeler & Shaw, 1995; Zedler & Kercher, 2005). For other areas (Types A and B), landscape-scale hydrological measures generally have to be taken to retain sufficient water, or to restore groundwater discharge patterns and related vegetation heterogeneity (Cooper *et al.*, 1998; Grootjans *et al.*, 2006; Bailey Boomer & Bedford, 2008; Smith *et al.*, 2008; Vitt *et al.*, 2011). As explained below, hydrogeochemical changes may impose constraints on hydrological measures, and water quantity issues should always be regarded in light of possible changes in groundwater and surface water quality, and of changes in soil type, structure and chemical quality (Lamers *et al.*, 2002a; Cusell *et al.*, 2013).

(3) Acid buffering

The ANC impact of a rise in water table in drained fens (Type B) that lack sufficient HCO_3^- and Ca buffering in their peats to prevent acidification strongly depends on whether the wetland will become flooded or not. As lateral water movement in the peat is slow due to its low hydrological conductivity, raising the water table in ditches and canals without flooding the fields will only gradually impact the meadows, and often only increases the ANC in the first couple of meters. If flooded in winter, infiltration can be very low, depending on the extent of hydrological recharge. It is therefore very hard to mimic the buffering effect of raised groundwater tables in the past by the use of surface water. If measures lead to an increase of the groundwater table, it is easier to restore ANC.

Different fen types show different types of hydrology. For carr woods in oxbow lakes, natural water-table fluctuation during the year and the flow-through of groundwater to surface water was shown to be essential for restoration (Lucassen *et al.*, 2005). Raising the surface water table all-year round as a rewetting measure for Type C fens led to large-scale eutrophication with phosphate, and toxicity of ammonium and sulfide. The outflow of nutrients and sulfate

was vital, and overly elevated surface water tables blocked the discharge of groundwater in the fen. Oxbow lakes turned into odiferous (sulfide-rich) locations completely covered with *Lemna* spp., while characteristic species including several *Carex* spp., and even *Alnus glutinosa* L. began to senesce. Another example showing the essential role that water-table fluctuation can play in ecosystem functioning is the restoration of species-rich riparian *Juncus-Molinia* fen meadows. These semi-natural, mown peat meadows harbor a great diversity of species in Europe, including many threatened species. Next to the specific edaphic and hydrological conditions, yearly mowing of these meadows is necessary to prevent the dominance of highly competitive species at the expense of lower, slow-growing species. Characteristic plant species of this community such as *Succisa pratensis* Moench and *Cirsium dissectum* (L.) Hill need naturally fluctuating groundwater tables to be lower in summer (5–40 cm below soil surface), also because they prefer nitrate over ammonium as an N source. During winter, however, high groundwater or surface water levels are needed to reload the base saturation of the Cation Exchange Capacity (CEC) and prevent drought-induced acidification in summer. If water tables are kept artificially high throughout the year, the vegetation type will change to *Carex*- or helophyte-dominated fens. These examples show that rewetting may not simply be a matter of raising the water table, but depends strongly upon the hydrological regime needed by the particular ecosystem type (Wheeler *et al.*, 2004). As each vegetation type requires its own water-table regime, this is an important issue for restoration; the creation of gradients at the landscape scale will ensure gradients in vegetation.

(4) Eutrophication as a constraint

As the agricultural use of fens decreased water levels to such an extent that direct conversion to more natural wetlands is no longer possible, rewetting seems to be the first logical action to take in Type B and C degraded fens. The problem however, is that the large amount of nutrients still present in the peat cannot be simply flushed away by rewetting (Smolders *et al.*, 2008). In Water Conservation Areas in the Everglades, concentrations of P in the surface water have remained the same in spite of a 50% reduction in P input, as a result of internal mobilization from the organic soil during flooding (Reddy & Rao, 1983; Richardson, 2008). As a result of fertilization legacies, fen restoration projects in both Europe and North America have often been compromised by the development of highly productive monocultures of species such as soft-rush *Juncus effusus* L. (Fig. 2), *Glyceria* spp. (including reed sweet grass) or cattail *Typha* spp., for which litter decomposition rates are high due to their chemical composition (Richardson, 2008; Smolders *et al.*, 2008).

High nutrient concentrations also lead to high nutrient availability (low C:P, low C:N ratios) in the peat, potentially accelerating decomposition rates and thereby retarding peat formation. Thatchers who use reed to cover the roofs of traditional farms in the Netherlands, for instance, have long known that if they use common reed *Phragmites australis* from



Fig. 2. Monoculture of fast-growing *Juncus effusus* L. after rewetting of agricultural peatland. Photo: L. Lamers.

very eutrophic locations, the roofs will decompose more quickly. However, despite intensive research, the effects of eutrophication on decomposition rates are still inconsistent (Kalbitz *et al.*, 2000). If peat contains high concentrations of P, pore water and surface water quality become adverse after rewetting due to the mobilization of P as a result of microbial Fe reduction. As reduced Fe compounds are less able to bind P, waterlogging or flooding will always lead to mobilization of Fe-bound P (Ponnamperuma, 1984; Lamers *et al.*, 1998a; Zak *et al.*, 2010). The rate of mobilization is determined by the fertilization history of the soils involved, in addition to the type of nutrient binding in the soil (Fig. 3). As Ca- and Al-bound iron P fractions are not redox sensitive, these P reservoirs will not respond to flooding. Post-rewetting, eutrophication is one of the major issues of former agricultural lands and for the restoration of surface waters (lakes, canals, ditches, peat extraction pits) in these areas, but advantageous management techniques can alleviate this problem to ensure successful rich fen restoration.

The eutrophying impact of adjacent intensive farming has to be eliminated, which can be a challenge for small-scale restoration projects in agricultural areas. This includes water-quality control, by choosing the best option for water supply and by hydrological uncoupling of adjacent fertilized areas (Richardson *et al.*, 2011). Such control may be difficult, as fen areas have always been used as a buffer in order to keep optimal agricultural hydrological regimes to prevent waterlogging or desiccation. In the Everglades, excess inputs of P from the northern agricultural areas constrain ecological restoration (Richardson, 2010). At the Ramsar Site, Weerribben-Wieden in the Netherlands, large fluxes of P are pumped in from the surrounding agricultural polders (areas in which water levels are actively kept lower) to the first water storage canals (Cusell *et al.*, 2014). The hydrological uncoupling of a number of polders has resulted in a significant decrease in P loading.

The lowering of the P input in fen surface waters may require additional purification, by phosphate stripping using Fe or Al salts applied to the water supply or *in situ*, or by constructed wetlands. If metals are applied *in situ*, gradual dosing is required to avoid strong acidification due to hydrolysis and to avoid toxicity (J. J. M. Geurts, personal communication). Natural wetlands can reduce both

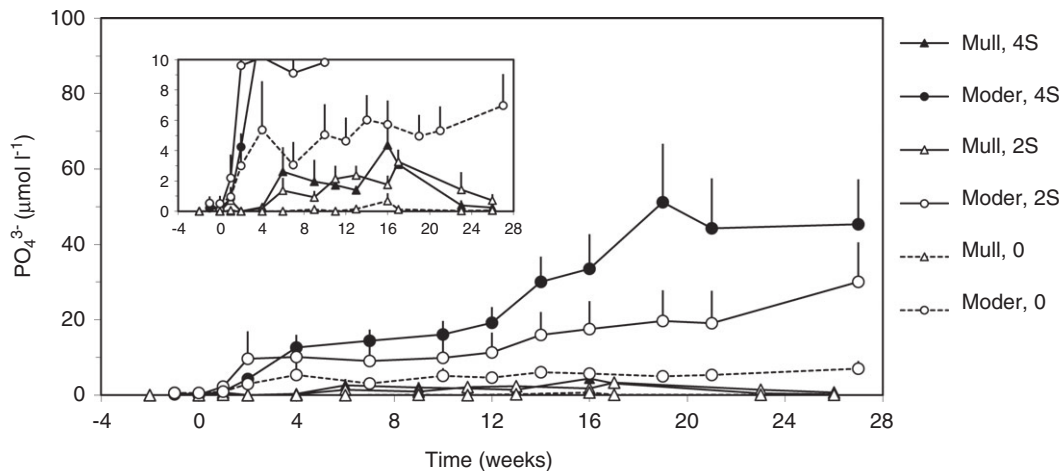


Fig. 3. Mobilization of phosphate in pore water of peat during experimental rewetting of peat monoliths from two peat meadows in the Netherlands (hydromull and hydromoder profiles). Triangles: low P availability; circles: high P availability. Dashed lines: without sulfate addition; solid lines: with sulfate addition [open symbols 2 mmol l^{-1} ($190 \text{ mg sulfate l}^{-1}$); filled symbols 4 mmol l^{-1} ($385 \text{ mg sulfate l}^{-1}$)]. Values are means + S.E.M. ($N = 5$ and 6 for Mull and Moder, respectively). After Lamers *et al.* (2001).

N and P levels from surface water (Fisher & Acreman, 2004). However, constructed wetlands on former fertilized farmland will work as purification plants with respect to nitrogen and organic compounds, but not for P-stripping (Richardson, 1985; Vymazal, 2007). In most of these constructed wetlands, P loading from the rewetted sediments to the water layer is much higher than the uptake of P by plants (even if they are regularly mown and removed), and the outflow contains high values of P unless special substrates are used to increase P sorption (Vymazal, 2007). In addition, high P concentrations in winter are unaffected. This is also an important risk for the outflow water from fens restored on P-polluted soils. For this reason, the inclusion of rewetted fens on P-rich soils without additional measures in the hydrological network of existing fens is advised against. One hectare of 'restored' fen can easily lead to eutrophication of many hectares of surface water in existing fens.

As surface waters, including former peat extraction sites (Type D degraded fens) in fen landscapes are generally shallow (0.1–1.5 m), high internal P loading from sediments has a strong effect on water quality. If the input of potential electron acceptors such as sulfate and nitrate is high, this should be tackled too as this may lead to internal eutrophication (Lamers *et al.*, 2002b). Internal P-loading can be reduced by the optimization of water quality (see above), dredging of the top layer, or internal P fixation. For internal fixation in fen water bodies, Fe or Al salts can be used (Cooke *et al.*, 1993; Boers *et al.*, 1994; Smolders, Nijboer & Roelofs, 1995), provided that the external loading with P (and S) is reduced as well. The effectiveness of removal of sludge (highly decomposed peat) strongly depends on the properties of the peat. After dredging of the top layer and installation of a P-stripping plant, the water quality of a large peat lake that had been suffering from cyanobacterial blooms became much better, but only for a couple of years. After this initial period, P-mobilization rates in the exposed P-rich layer became

very high, resulting in extremely high P concentrations of $50 \mu\text{mol l}^{-1}$ (1.6 mg P l^{-1}), triple the original value (Michielsen, Lamers & Smolders, 2007). This example highlights the importance of preliminary investigations to help prevent an extremely high cost to benefit ratio. If peat quality is better, and the required hydrological and hydrochemical conditions are met, dredging can result in the restoration of biodiverse plant and fauna communities in fens. The Fe:P ratio of the pore water can be used as a simple proxy to estimate P fluxes from the peat sediment to the surface water layer as the availability of Fe strongly determines P fixation at the sediment–water layer (Geurts *et al.*, 2008). Costly biomanipulation (fish removal) in fen water bodies (ditches, lakes) is often insufficient for sustainable restoration, because external and/or internal nutrient loading, remigration of planktivorous and benthivorous fish, development of inedible cyanobacteria blooms, or wind movement will easily lead to a flip back to the turbid state with low biodiversity (Lamers *et al.*, 2002b).

(5) Eutrophication risk assessment

The potential risk of not only developing a hypertrophic area, but also creating a significant new source of nutrients has to be assessed before the transformation of agricultural lands to natural fens in Type B deteriorated fens. Three options are available: (i) to create hypertrophic fens with low biodiversity for decades or longer, (ii) to remove the hypertrophic top layer, or (iii) to leave the area dryer and remove nutrients by phytoextraction. The latter option (Novak & Chan, 2002), needed to reduce P availability and avoid low biodiversity, will not be discussed here.

In eutrophic fen meadows, past application of fertilizers and high-nutrient floodwater make restoration very challenging and topsoil removal is essential to create a favorable starting point to restore biodiversity (Van Dijk *et al.*, 2007; Smolders *et al.*, 2008; Zak *et al.*, 2010). In this way succession

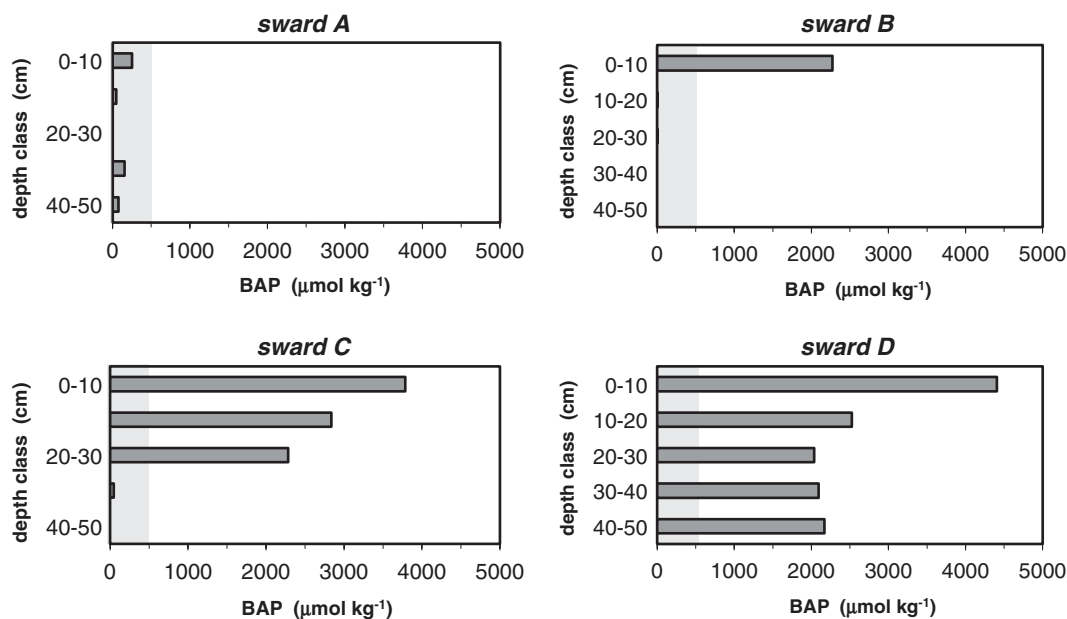


Fig. 4. Depth profiles for biologically available phosphorus in the soils of four peat swards in the same area (equal geological fen peat deposits) with increasing fertilization histories (A–D). Shading shows reference values for fens with high biodiversity. BAP, biologically available phosphorus (lactate-acetate extract according to Egnér, Riehm & Domingo, 1960). L. P. M. Lamers (unpublished results).

can be reset, and the peat layer that has suffered from irreversible physical changes due to desiccation is removed. The level of eutrophication of the top layer, and its depth, will vary strongly depending on the intensity of fertilization in the past, peat type and hydrology. Figure 4 shows the depth profiles of biologically available P in agricultural fens, and the reference value ideal for high biodiversity. From such profiles, it becomes clear that the depth of the layer to be removed may vary between 10 cm and more than 50 cm. Although peat removal may seem odd as part of fen creation, it must be realized that P levels are often high enough to create hypertrophic fens for decades or even centuries, even if P is being removed by water flow or mowing and hay removal. Prescreening of depth profiles for biologically available P can show whether topsoil removal is feasible, and to what depth. Alternatives to topsoil removal in order to lower P availability, such as the addition of iron, calcium or even lanthanum-modified clay, have been shown to fail (Geurts *et al.*, 2011). As phosphate as a fertilizer is rapidly becoming scarcer at a global scale, techniques to recover P from heavily fertilized soils (similar to those for sewage sludge and manure) will become economically more feasible and may be applied to cover restoration costs in the near future.

V. BIODIVERSITY: SPECIES RECOLONIZATION

(1) Habitat fragmentation

The restoration of habitat quality is a major issue, but can never be separated from the fact that recolonization by target species may be difficult, if not impossible, in heavily

fragmented areas such as agricultural lands where these species have disappeared (Saunders, Hobbs & Margules, 1991; Bakker *et al.*, 1996). The diaspore bank can be assessed by analysis of its viability (Thompson, Bakker & Bekker, 1997; Ter Heerdt, Schutter & Bakker, 1999). However, after intensive agricultural use, the vegetation mat is generally closed and the diaspore bank only contains very common, fast-growing species with long-term-persistent seeds (Bekker *et al.*, 1997; Klimkowska *et al.*, 2007, 2010). The longevity of the seeds of many characteristic and rare plant species is less than 5 years (transient and short-term persistent), and recolonization after restoration is only possible by dispersal, or by clonal growth if target species are still present (Gignac *et al.*, 2004; Middleton *et al.*, 2006; Van Dijk *et al.*, 2007). However, many species are wind dispersed and can only travel less than 1 m or a few meters per year (Harper, 1977; Strykstra, Bekker & Bakker, 1998), provided that habitat quality is sufficient (which is not the case for croplands). Although wind dispersal can also span more than 100 m (Portnoy & Willson, 1993), this is generally too short a distance to allow for recolonization after restoration measures in highly fragmented agricultural landscapes (Soons *et al.*, 2005). Even for meadow thistle *Cirsium dissectum* (L.) Hill, a wetland species with plumed seeds, the probability of dispersing 100 m is very low (Soons *et al.*, 2004). If a few seeds reach the restored sites, colonization of this particular species is still possible, but not for most other species of the community with other life-history traits. In highly fragmented landscapes, however, even colonization by long-distance wind-dispersed plants is very unlikely (Soons *et al.*, 2005). For water- and animal-dispersed plants, dispersal distances are in the range of many kilometers, and have even been shown to

be 100 s of kilometers (Sorensen, 1986; Boedeltje *et al.*, 2003). Distribution of the various fen species strongly depends on seed buoyancy, and can be greatly hampered by intensive water management in agricultural areas (Van den Broek, Van Diggelen & Bobbink, 2005). However, despite better connectivity, adverse habitat quality including the presence of dense vegetation may still prevent recolonization of fens (Grime, 1974; Van Dijk *et al.*, 2007; Sarneel *et al.*, 2011).

(2) Species reintroduction

If viable target species are absent, which is generally the case in arable fields, and dispersal is impossible due to habitat fragmentation, even perfect habitat restoration will not lead to the return of target vegetation types. This implies that restoration projects should by definition take possible constraints for recolonization into account before defining management plans, and the conservation of species-rich fen types should be given high priority. If more natural recolonization of target plant species is highly improbable, the species can be reintroduced after the restoration of their habitat by the application of hay, seeds and spores, seedlings or plants from donor sites (Van Groenendael, Ouborg & Hendriks, 1998). In order to select locations for restoration, the probability level of recolonization should therefore be estimated, similarly to the probability level of restoring habitat quality.

The reintroduction of plant species in fens ranges from actively transporting a complete fen, through the option of planting sedges or reedlands, to the spreading of seeds. In the case of planting, intensive herbivory by geese, other wetland birds and fish has been shown to be a serious problem, which can only be solved by the use of netting in the initial stages (E. S. Bakker, personal communication). In a fen restoration project in cut-away peatlands in Quebec (Type A), the application of donor propagules including seeds, rhizomes and moss fragments appeared to be highly effective for the reintroduction of vascular plants (Cobbaert, Rochefort & Price, 2004). Fen mosses may well regenerate from fragments applied if there is a canopy of vascular plants (Graf & Rochefort, 2010). For most species, a closed vegetation mat of highly competitive species is a major constraint (Van Dijk *et al.*, 2007). After the removal of the nutrient-rich topsoil and application of hay, Patzelt, Wild & Pfadenhauer (2001) were able to restore 70% of the species from the donor site on a formerly drained fen (Type B, seminatural fen meadow). As most fen species had dormant seed banks, fluctuations of temperature and light were needed to break seed dormancy. The use of propagules including those in hay may, however, give variable results, depending on seed viability and germination conditions (Graf & Rochefort, 2008). The reintroduction of individuals of *Scorpidium scorpioides* (Hedw.) Limpr., an endangered moss species in European semi-natural rich fens, was shown to be highly effective (Kooijman, Beltman & Westhoff, 1994). In addition, the introduction of fragments of this species and several other fen bryophytes can be very effective for restoration (Malson & Rydin, 2007). In

their review on plant species introduction in restoration programs for managed grasslands in Europe, Kiehl *et al.* (2010) show that the spreading of seeds, hay or soil from donor sites can be successful, but only after topsoil removal or tilling. For older ex-arable sites overgrown by weeds, introduction was much less successful. These results underscore the strong interactions between habitat quality, species interactions, management and dispersal. Management (mowing) may prevent dominance of species due to high nutrient availability, but once highly competitive species have become dominant, introduction will become difficult if not impossible.

Although the introduction of seeds may seem a modern measure, in many countries animals, including domestic cattle, acted as vectors for a long time before large-scale land-use change. This vector service has, at a much smaller scale, been taken over by mowing machines used to maintain high species diversity by disturbance, preventing dominance of highly competitive species (Strykstra, Verweij & Bakker, 1997). For some fen species, it was shown that seeds from small populations had much lower vitality due to inbreeding depression (Vergeer *et al.*, 2003; De Vere *et al.*, 2009). As the germination and settlement of seedlings is often the most sensitive part of the life cycle, genetic variability plays an important role in conservation biology (Ouborg, Vergeer & Mix, 2006). Although the dispersal of animals may seem less restricted, habitat fragmentation is well known to be a problem here as well, depending on their mobility and life strategies, and on the level of habitat fragmentation (Zedler & Kercher, 2005).

In addition to dispersal-related constraints, plant species colonization can also be problematic because of space and light deprivation. The restoration of species-rich margins of fen water bodies (Type D) appears to be a much bigger challenge than the restoration of their aquatic vegetation, because they are often dominated by fast-growing helophyte species such as *Phalaris arundinacea* L., *Phragmites australis* (Cav.) Trin. Ex Steud, *Typha latifolia* L. or *Typha domingensis* Pers. (Craft *et al.*, 1995). Their dense biomass and clonal reproduction leave little space and light available for the germination of seeds and settlement of seedlings (Maurer & Zedler, 2002; Kotowski & Van Diggelen, 2004). Higher availability of nutrients may also increase the risk of dominance of highly competitive invasive species.

VI. RESTORATION OF CARBON SEQUESTRATION AS AN ECOSYSTEM SERVICE

(1) Restoration of the terrestrialization process and peat accumulation

An interesting aspect of rich fens is their succession from open water to terrestrial vegetation on dead biomass (peat). The restoration of fens is, therefore, not only the rehabilitation of different communities at the spatial scale, but also restoration on the temporal scale including terrestrialization and the

peat-forming process. This target can become a greater challenge than species recolonization, especially if high nutrient levels as a legacy of agricultural use speed up decomposition.

The initial situation strongly determines restoration prospects. At Type A locations, former fen locations where all peat has been extracted to other soil layers (sand, clay), mire formation (i.e. with active peat formation) will be much more difficult. The initial stages after rewetting may not directly lead to peat production, but for instance to waters dominated by charophytes. As a result of peat extraction, the historical hydrology has often been heavily modified, and recharge fluxes may have become much larger. In other areas (Types B and C), the original discharge fens have been replaced by high-recharge locations after rewetting measures, or water levels and/or hydroperiodicity have been modified.

(2) Greenhouse gas balance

C losses to the atmosphere of drained peatlands in Europe are high, and measured fluxes range between +80 and +880 g C m⁻² year⁻¹, with an average around +400 g C m⁻² year⁻¹ (Nykänen *et al.*, 1995; Kasimir-Klemedtsson *et al.*, 1997; Joosten & Clarke, 2002; Byrne *et al.*, 2004; Freibauer *et al.*, 2004; Jacobs *et al.*, 2007; Berglund & Berglund, 2010; Drewer *et al.*, 2010), corresponding to a global warming potential (GWP) of +290 to +3230 g CO₂ eq m⁻² year⁻¹. Emissions of CH₄ are low due to drainage (Gorham, 1991; Freibauer *et al.*, 2004). Subsidence rates measured in Sweden were (after the first consolidation) 0.5 cm year⁻¹ for extensively managed pastures, 1 cm year⁻¹ for fertilized haylands, 1.5 cm year⁻¹ for cereals, and even 2.5 cm year⁻¹ (2.5 m per century) for intensively cultivated crops such as potatoes (Berglund & Berglund, 2010). Average greenhouse gas emissions from agricultural peat soils are 350 g C m⁻² year⁻¹ for grasslands and 490 g C m⁻² year⁻¹ for croplands. The use of peatlands for row crop production (e.g. potato, sugar beet) shows extremely high C losses of +380–950 g C m⁻² year⁻¹, and is therefore by far the least sustainable land use (Freibauer *et al.*, 2004).

Measurements of C fluxes after fen restoration (rewetting) are, however, scarce. For an ex-arable fen meadow that had been rewetted 10 years before and became dominated by *Phragmites australis* (Cav.) Trin. Ex Steud, Hendriks *et al.* (2007) measured a NEE of, on average, -280 g C m⁻² year⁻¹ (-1030 g CO₂ m⁻² year⁻¹). Although one has to be careful to draw far-reaching conclusions, also because of uncertainties related to the use of different techniques, these high values indicate there is great potential for C storage on abandoned peatlands (Graf & Rochefort, 2009). Even if rewetting does not lead to the values (-5 to -40 g m⁻² year⁻¹) found in undrained fens, C losses to the atmosphere as compared to intensive agricultural use, will still be much lower. An important problem is the fact that peatlands still show hotspots of C loss after rewetting, due to high phenolic oxidase activities and related high rates of organic matter breakdown (Fenner *et al.*, 2011). As a result of the build-up of labile carbon fractions and nutrients during drought, high amounts of

carbon can be lost to the atmosphere, groundwaters and surface waters after rewetting (Fenner & Freeman, 2011). This is further enhanced by the increase in pH as a result of alkalinity generation due to anaerobic reduction processes, which may even stimulate decomposition rates. In addition, this decrease in acidity is known to lead to higher exports rates of DOC, as a result of changes in both decomposition rates and DOC solubility. These processes may lead to unexpected and disappointing results in the first years after rewetting. Recent ideas to increase C sequestration in peatlands even suggest the addition of phenolic compounds to reduce decomposition (Freeman, Fenner & Shirsat, 2012), which could be an interesting idea to compensate for high C losses due to eutrophication and water table decline before restoration. The benefits of carbon offsetting can be used to finance fen restoration (Worrall *et al.*, 2009). In fen meadows that have become acidic as a result of drainage, however, decomposition rates may also increase initially after rewetting as a result of high nutrient values and increased ANC (Van Dijk *et al.*, 2004).

As CH₄ production increases exponentially with an increase in water level, rewetting of drained fens will lead to a strong increase in CH₄ emission, from values around 0 (including negative values due to CH₄ oxidation) to values in the range found for peatlands that have been less influenced by human activity. As the 100 year GWP of CH₄ is 25 times that of CO₂ (on a mass basis; Solomon *et al.*, 2007), it is important to incorporate its impact on global warming. Recently, it has been estimated that the CH₄ output of global wetlands reduces the effects of the continental C sink by 25% (Bastviken *et al.*, 2011). Around 90% is emitted by open water, of which half is by ebullition, and 10% through plants (Bastviken *et al.*, 2011). Emergent species strongly facilitate the emission of CH₄ from peat by their funneling effect (flow through internal air channels) and by stimulation of methanogenesis, with fluxes ranging from 8 to 260 mg C m⁻² day⁻¹ largely determined by temperature and water table (Bubier, 1995; Nykänen *et al.*, 1995; Bellisario *et al.*, 1999; Bastviken *et al.*, 2011). On a yearly base, fens emit 5–50 g CH₄-C m⁻² (Byrne *et al.*, 2004), which corresponds to a GWP of 165–1650 g CO₂ eq m⁻² year⁻¹. Post-restoration changes in vegetation have a significant impact on CH₄ emission rates (Waddington & Day, 2007; Bhullar *et al.*, 2014), as has herbivory (Dingemans, Bakker & Bodelier, 2011). In addition, water quality can strongly influence CH₄ emissions, as concentrations and reduction rates of SO₄²⁻ can be high after rewetting (Lamers *et al.*, 1998a), and inhibit methanogenesis (Kang, Freeman & Lock, 1998). In restored fens, CH₄ fluxes seem to be in the high range of more pristine fens but higher than in cutover minerotrophic peatlands, as shown in Canada (Mahmood & Strack, 2011). Increased sulfate inputs from S deposition, or from surface water or groundwater will strongly suppress CH₄ emissions from peatlands (Vile *et al.*, 2003). Atmospheric S pollution may reduce global CH₄ emissions from wetlands by 15% (Gauci *et al.*, 2004).

Despite increased CH₄ emission and, to a minor extent, N₂O emission, rewetting of formerly arable, eutrophic

fen peatland can still generate a net sink for greenhouse gases with GWP values around $-85 \text{ g CO}_2 \text{ eq m}^{-2} \text{ year}^{-1}$ (Hendriks *et al.*, 2007). For undrained European fens, a large range has been reported from -25 (reduction of global warming) to $+150 \text{ g CO}_2 \text{ eq m}^{-2} \text{ year}^{-1}$ (stimulation of global warming), although many values have a high level of uncertainty (Byrne *et al.*, 2004). It can be expected that high nutrient levels in rewetted ex-arable lands will stimulate decomposition. Literature results, however, are contrasting and include stimulation of decomposition, no effect, and even higher peat accumulation rates (Richardson & Marshall, 1986; Aerts & Toet, 1997; Kalbitz *et al.*, 2000; Sarneel *et al.*, 2010).

The effect of simultaneous increases in temperature and CO_2 on peat formation in fens also is a subject of debate. The discussion is due to the fact that these changes may lead to higher decomposition rates as a result of higher temperatures, but also to higher primary production rates, which may offset each other (Gorham, 1991; Kirschbaum, 2000). However, there are also higher risks of drought episodes, stimulating decomposition and reducing fen plant growth (Ise *et al.*, 2008). In addition, CH_4 emissions can increase, not only due to higher temperature but also as a result of raised CO_2 levels. It is also alarming that the microbial decomposition of biogeochemically recalcitrant organic matter is more sensitive to increased temperature than that of more readily decomposable organic matter (Craine, Fierer & McLaughlan, 2010). More research is needed to be able to estimate and predict the interacting effects of rewetting, eutrophication and climate change on decomposition, net ecosystem carbon exchange and peat formation after restoration of fens, because the interaction between these processes may lead to a trade-off in ecosystem services. With respect to greenhouse emissions, it is clear that the rehabilitation of vegetated areas instead of lakes is preferred. Although peat lakes increase the water storage capacity, they are also hotspots of CH_4 emissions with very low CO_2 -fixation rates. For biodiversity, however, landscape and habitat diversity including open water is important.

VII. POLICY ISSUES

(1) Spatial and temporal scales

The restoration of fens has multiple spatial scales. As fens depend on water supply, rewetting will always require landscape-scale measures (Hobbs & Norton, 1996; Bedford, 1999; Richardson *et al.*, 2011), such as management of water abstractions from rivers and groundwater feeding the fens (Acreman & McCartney, 2009). This particularly holds for severely drained fens (Type B), but also for less severely drained fens with modified hydrology (Type C) and excavated fens and oil-sand pits (Type A). Such a mandate automatically implies that efforts call for close cooperation between water and nature managers, with respect to both

water quantity and quality. In some cases restoration is being attempted at the landscape scale, such that much of the wetland's catchment is included, for example the Great Fen Project in the UK. At a smaller scale, topsoil removal may be required to prevent hypertrophic conditions, and the reintroduction of species may be necessary. At a temporal scale, initial efforts will be most resource intensive, especially when additional measures to prevent eutrophication and ensure recolonization are needed in concert with hydrological measures. In eutrophic fen waters (Type D), dredging is generally necessary to prevent both eutrophication due to internal nutrient mobilization and turbidity due to high resuspension of particulate organic matter preventing aquatic macrophyte development and terrestrialization.

(2) Conflicting targets

As stated, the aim to recreate biodiverse fens may not always be consonant with the aim to have high C-sequestration rates in fens, as high production rates generally lead to low biodiversity. Depending on the target vegetation and fauna, annual mowing may even be necessary to prevent dominance of highly competitive species in eutrophic areas. This, however, will strongly reduce peat production, but may be necessary because intermediate successional phases have become rare, and their species are endangered. As long as there is no guarantee that new succession (terrestrialization) will take over these refugee areas, and that they are sufficiently connected to donor sites, management may opt for biodiversity at the expense of faster peat formation.

An additional point of concern about restoration targets, which often leads to disagreement between ecologists, is that highly productive fens may provide habitats for marshland birds, but have low overall biodiversity. In Europe, coastal agricultural peat meadows that are still being fertilized provide the most important habitat for a number of red list bird species such as black-tailed godwit *Limosa limosa* (L.) that are important in Natura 2000 legislation. This target, however, leads to further land subsidence in areas that are already far below sea level. Although lower levels of fertilization are also required for meadow birds to create more biodiverse swards with higher insect densities to feed offspring (Vickery *et al.*, 2001), relatively low water tables will still lead to further carbon losses. The alternative would be to rewet these lands and create peat-forming fens, and lose the threatened bird species. This example shows that it may be difficult to set targets for fen restoration.

The combination of agriculture and nature conservation is complicated. Although hundreds of millions of euros and dollars per year are spent on financial compensation to farmers to change their practices for ecological benefit (Farm Bill USA, Agri-Environmental Scheme Europe), the gain for biodiversity of these subsidies appears to be highly variable (Zedler, 2003; Kleijn *et al.*, 2006). This indicates that spatial segregation between intensive farming and nature reserves may be the most feasible option. Only agricultural lands that occur in heterogeneous landscapes, do not receive high rates

of fertilization and have not been extensively drained (as in the past) can be expected to support high biodiversity, unless additional management is being carried out.

(3) Land-use challenges

In the past, policy promoted and subsidized land-use change from 'useless' wetlands (including fens) to arable land and meadows. The conversion of fens that were generally seen as a threat (flooding, drowning, diseases, monsters, ghosts), has a long tradition and communities have put much effort into creating new agricultural lands. It is therefore understandable that local communities may be opposed to rewetting projects, even if it is clear that the agricultural use of these areas is no longer economically feasible. The local communities in adjacent areas fear flooding of their properties (including farmland), irreversible damage of infrastructure (embankments, building constructions), undesired species (plants and animals) and mosquito plagues (Willot, 2004).

Restoration may lead to conflicting ecosystem services, e.g. rewetting can be beneficial for the increase in biodiversity, but can simultaneously lead to loss of its storm water storage capacity and increased flooding risks for people. The creation of large highly productive, monospecific *Phragmites* spp. fens may be unattractive to botanists, but will provide an important fen habitat for many marshland bird species, including endangered species. To deal with these contrasting ecosystem services, Acreman *et al.* (2011) provided a synergistic approach to address the different ecosystem services of the Somerset wetlands, and indicated that a trade-off model for management decisions (those including restoration) was vital. Conflicts among ecosystem services and among different stakeholders show that the governance aspects of the restoration of rich fens and fen water bodies are important and should be addressed prior to the implementation of restoration programs. Good contact with local authorities and local communities, and proper information supply and participation is an essential part of fen restoration, often overlooked by nature managers and water managers. The participation of the community has to be initiated before the start of the projects (seminars, documentation), to make it become their project too. Restoration projects can easily be incorporated into school projects, by letting children monitor the changes in their own fen in their biology programs.

(4) Restoration costs

Wetlands represent 40% of all ecosystem services globally, of which 40% is provided by inland wetlands (Zedler & Kercher, 2005). The value of intact wetlands such as fens, including the values of all of their ecosystem services, has been estimated at 6000–45000 \$ ha⁻¹ year⁻¹ (Costanza *et al.*, 1997; Millennium Ecosystem Assessment, 2005; Zedler & Kercher, 2005). For drylands, by contrast, the value is only 200–300 \$ ha⁻¹ year⁻¹. The replacement costs for water purification by the construction of water treatment plants, for

instance, ranges between 5000 and 7000 \$ ha⁻¹ year⁻¹. For Canadian wetlands, sustainably managed intact areas have been calculated to represent 6000 \$ ha⁻¹ year⁻¹, against 2000 \$ ha⁻¹ year⁻¹ for intensive farming (Balmford *et al.*, 2002). Although restoration costs may seem high, it has been estimated that the benefit:cost ratio for restoration is still around 6 for inland wetlands, and may even reach values of around 75 for grasslands (R. S. De Groot, personal communication). Although restoration is possible, many changes are expected to be irreversible (Zedler & Kercher, 2005), underscoring the need for protection of wetlands including fens that have not, or have to a minor extent, been influenced by anthropogenic forcing, and emphasizing that peat extraction from pristine fens and other peatlands is ecologically undesirable.

VIII. FUTURE DIRECTIONS

(1) From trial and error to predictability

A key problem in fen restoration is the myriad of outcomes after rewetting (Schrautzer, Asshoff & Muller, 1996; Klimkowska *et al.*, 2010), as discussed above. Although the database of restoration projects provides indispensable insights, the results will only give correlative information based on trial and error, which makes it hard to explain the factors and processes driving various degrees of deterioration and variable success of restoration. In addition, one of the main problems of many fen-restoration efforts has been that they have not been monitored effectively or for a long period, and sometimes not at all. Reliable data are in short supply and particularly the starting conditions are often poorly recorded, sometimes not even really known.

To be able to predict the prospects for restoration of areas, choose the optimal set of measures, minimize cost to benefit ratios and make policy decisions about location choices, knowledge about key factors and key processes at different scales is vital (Zedler, 2000; Van Diggelen, Grootjans & Harris, 2001; Zedler & Kercher, 2005; Hein *et al.*, 2006). This calls for a good monitoring program and for the integration of biogeochemistry (cycling of water and elements), plant and animal sciences (species responses, ecogenetics and community development), landscape ecology (geohydrology, heterogeneity of habitat types and creation of gradients) and social sciences (environmental economics, governance). We promote the combination of correlative field research, experimental research in the field and experimental research under more controlled conditions to be able to determine causal relationships. In this way, field results from one area can be extrapolated to other restoration areas. Figure 5 shows an example of the incorporation of these variables into a decision-support system for fen restoration. Costs of preliminary examination and experiments are only a small fraction of the project costs, and will prevent unexpected and unwanted results.

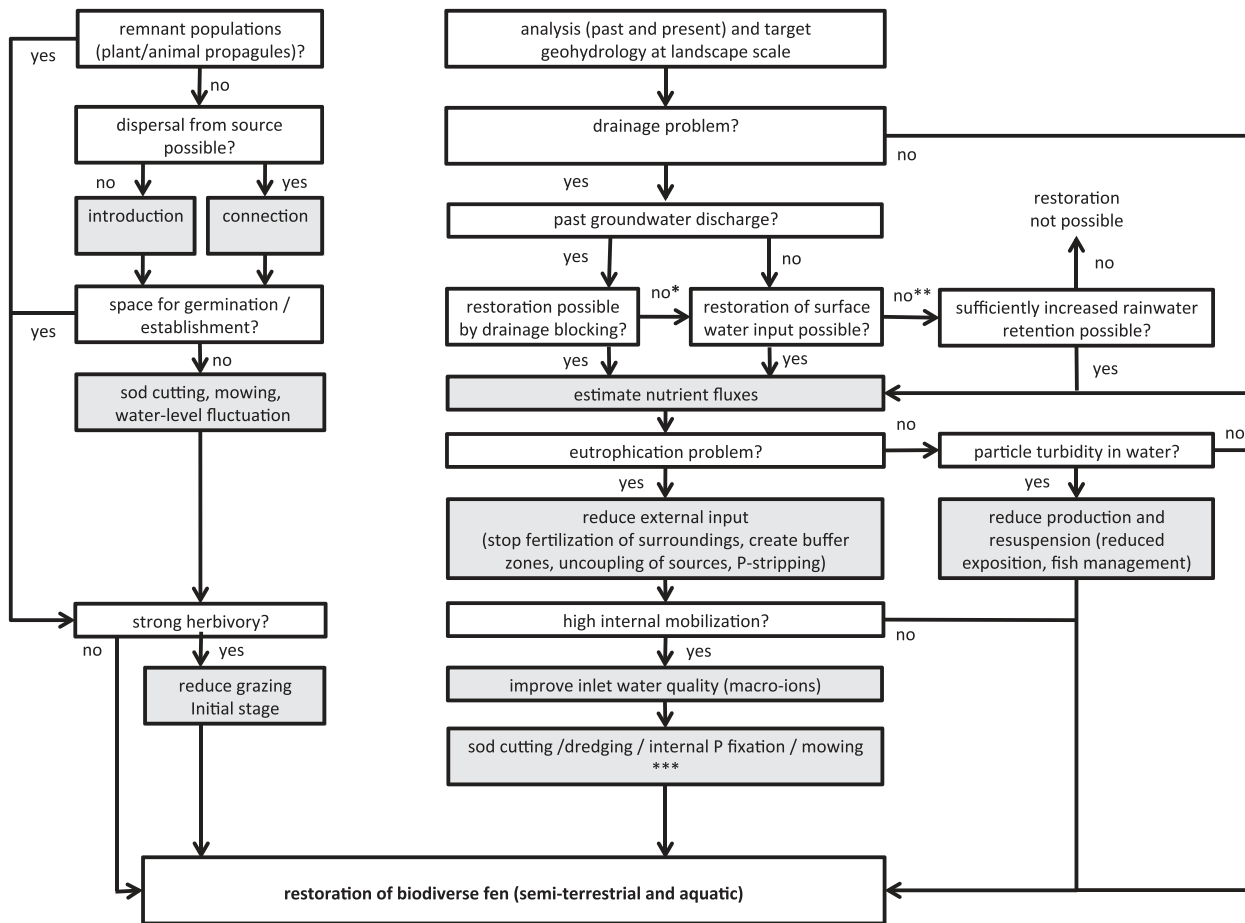


Fig. 5. Schematic representation of fen restoration measures. Note that measures for introduction of species (left side) and habitat restoration (right side) may both be required. Under very eutrophic conditions species introduction has little or no success. Measures are indicated by shaded boxes. * Compensation of groundwater influx by surface water influx will generally lead to species changes, ** compensation of groundwater influx by increased rainwater retention will lead to species changes (see text). *** If eutrophic peat is not removed, a highly productive fen with low species diversity will result after hydrological measures, with high P fluxes downstream.

(2) Fen restoration in a changing climate

Not only the large-scale loss of biodiversity from the landscape down to the species scale, but also the loss of other significant ecosystem services (Table 1), including hydrological buffering of changes in water supply, nutrient sequestration, carbon storage, and recreational functions, call for integrated, landscape-scale restoration programs in North America and Europe, and in other parts of the world. Higher atmospheric CO₂ concentrations, temperatures and incidence of extreme weather conditions (including droughts and heavy rainfalls; Solomon *et al.*, 2007; Strack, 2008) will only further increase this sense of urgency for fen restoration, in which wetland scientists, water managers, nature managers, social scientists, and policy makers have to cooperate to develop and carry out well-considered projects with high benefit to cost ratios. The effects of climate change on C exchange in fens will be determined by the combined effects of changes in temperature (including more extreme drought and rainfall episodes), changes in primary

production as a result of rising temperature and CO₂ levels, and changes in decomposition rates as a result of changes in water table, water chemistry and temperature, and litter quality as a result of vegetation changes. Forecasts for global-change effects on different fens may therefore vary widely. Interestingly, Fan *et al.* (2013) recently predicted (based on a calibrated model) that a boreal rich fen in Alaska will first increase its C sink function between 2012 and 2061, because primary production will benefit relatively more, and will subsequently switch to a C source between 2062 and 2099 because the scale will tip to dominance of decomposition.

IX. CONCLUSIONS

(1) Fens represent a large array of ecosystem services, including the highest biodiversity found among wetlands, hydrological services, water purification and carbon sequestration.

(2) Large-scale land-use changes including agriculture, and concomitant drainage has severely damaged or annihilated these services in many parts of North America and Europe; restoration plans are urgently needed at the landscape level.

(3) The restoration of damaged fens, including (A) excavated fens and oil-sand pits, (B) severely drained fens used as farmland, (C) less severely drained fens with modified hydrology, and (D) dredged fen waters, can be very successful, if both quantitative and qualitative geohydrology can be restored. However, we feel that it is essential to move on from a trial-and-error approach to a method enabling planning projects at the landscape scale based on prospects and chances, rather than historical frameworks.

(4) Before starting a project, the potentials related to the particular starting conditions and related targets have to be clear. Based on this assessment, the optimal restoration strategy must be chosen. It may be impossible to restore the various ecosystem services, so choices have to be made. In addition, different ecosystem services can be conflicting, calling for a trade-off analysis. If the required improvement of the starting conditions is impossible, the project should even be abandoned in favor of projects with higher potential.

(5) By monitoring and by preliminary research and experimental testing, aiming at key parameters and key processes in ecosystem functioning, fen restoration can become more predictable and much more cost effective, and ecological and economic disappointments can be avoided to a large extent. Restoration always has two pillars that must be addressed together in a decision-support system: habitat rehabilitation and species recolonization. Both issues may require additional measures, depending on the actual starting conditions.

(6) The creation of wet areas affects a large community in highly populated agricultural areas, and may cause conflicts because it counteracts past investments in the creation of arable land. Therefore, communication with and participation of the local authorities and community are essential for successful restoration.

(7) Although restoration measures may seem costly, both the ecological and the real economical value of restored fens are generally much higher than that of agricultural land, and cost to benefit ratios are low. Some of these values (e.g. C offsetting) can be used directly to finance restoration programs.

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XI. REFERENCES

- ACREMAN, M. C., HARDING, R. J., LLOYD, C., MCNAMARA, N. P., MOUNTFORD, J. O., MOULD, D. J., PURSE, B. V., HEARD, M. S., STRATFORD, C. J. & DURY, S. J. (2011). Trade-off in ecosystem services of the Somerset Levels and Moors wetlands. *Hydrological Sciences Journal* **56**, 1543–1565.
- ACREMAN, M. C. & MCCARTNEY, M. P. (2009). Hydrological impacts in and around wetlands. In *Wetlands Handbook* (eds E. MALTBY and T. BAKER), pp. 643–666. Blackwell, Oxford.
- AERTS, R. & TOET, S. (1997). Nutritional controls on carbon dioxide and methane emission from *Carex*-dominated peat soils. *Soil Biology and Biochemistry* **29**, 1683–1690.
- AERTS, R., VERHOEVEN, J. A. & WHIGHAM, D. F. (1999). Plant-mediated controls on nutrient cycling in temperate fens and bogs. *Ecology* **80**, 2170–2181.
- ARMSTRONG, J., AFREEN-ZOBAYED, F. & ARMSTRONG, W. (1996). Phragmites die-back: sulphide and acetic acid induced bud and root death, lignifications, and blockages within aeration and vascular systems. *New Phytologist* **134**, 601–614.
- BAILEY BOOMER, K. M. & BEDFORD, B. L. (2008). Influence of nested groundwater systems on reduction-oxidation and alkalinity gradients with implications for plant nutrient availability in four New York fens. *Journal of Hydrology* **351**, 107–125.
- BAKKER, J. P., POSCHLOD, P., STRYKSTRA, R. J., BEKKER, R. M. & THOMPSON, K. (1996). Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* **45**, 461–490.
- BALMFORD, A., BRUNER, A., COOPER, P., COSTANZA, R., FARBER, S., GREEN, R. E., JENKINS, M., JEFFERISS, P., JESSAMY, V., MADDEN, J., MUNRO, K., MYERS, N., NAEEM, S., PAAVOLA, J., RAYMENT, M., ROSENDO, J., ROUGHGARDEN, K., TRUMPER, K. & TURNER, R. K. (2002). Ecology – economic reasons for conserving wild nature. *Science* **297**, 950–953.
- BARTSCH, I. & MOORE, T. R. (1985). Preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebec. *Canadian Journal of Botany* **63**, 1241–1248.
- BASTVIKEN, D., TRANVIK, L. J., DOWNING, J. A., CRILL, P. M. & ENRICH-PRAST, A. (2011). Freshwater methane emissions offset the continental carbon sink. *Science* **331**, 50.
- BEDFORD, B. L. (1999). Cumulative effects on wetland landscapes: links to wetland restoration in the United States and southern Canada. *Wetlands* **19**, 775–788.
- BEDFORD, B. L. & GODWIN, K. S. (2003). Fens of the United States: distribution, characteristics, and scientific connection versus legal isolation. *Wetlands* **23**, 608–629.
- BEDFORD, B. L., WALBRIDGE, M. R. & ALDOUS, A. (1999). Patterns in nutrient availability and plant diversity of temperate North American wetlands. *Ecology* **80**, 2151–2169.
- BEKKER, R. M., VERWEIJ, G. L., SMITH, R. E. N., REINE, R., BAKKER, J. P. & SCHNEIDER, S. (1997). Soil seed banks in European grasslands: does land use affect regeneration perspectives? *Journal of Applied Ecology* **34**, 1293–1310.
- BELLISARIO, L. M., BUBIER, J. L., MOORE, T. R. & CHANTON, J. P. (1999). Controls on CH₄ emissions from a northern peatland. *Global Biogeochemical Cycles* **13**, 81–91.
- BELTMAN, B., VAN DEN BROEK, T., BLOEMEN, S. & WITSEL, C. (1996). Effects of restoration measures on nutrient availability in a formerly nutrient-poor floating fen after acidification and eutrophication. *Biological Conservation* **78**, 271–277.
- BERGLUND, O. & BERGLUND, K. (2010). Distribution and cultivation intensity of agricultural peat and gytja soils in Sweden and estimation of greenhouse gas emissions from cultivated peat soils. *Geoderma* **154**, 173–180.
- BHULLAR, G. S., EDWARDS, P. J. & OLDE VENTERINK, H. (2014). Influence of different plant species on methane emissions from soil in a restored Swiss wetland. *Plos ONE* **9**, e89588. (doi: 10.1371/journal.pone.0089588).
- BOBBINK, R., HORNUNG, M. & ROELOFS, J. G. M. (1998). The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural vegetation – a review. *Journal of Ecology* **86**, 717–738.
- BOEDELTEJE, G., BAKKER, J. P., BEKKER, R. M., VAN GROENENDAEL, J. M. & SOESBERGEN, M. (2003). Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. *Journal of Ecology* **91**, 855–866.
- BOERS, P., VAN DER DOES, J., QUAAK, M. & VAN DER VLUGT, J. (1994). Phosphorus fixation with iron(III)chloride—a new method to combat internal phosphorus loading in shallow lakes. *Archiv für Hydrobiologie* **129**, 339–351.
- BONN, A., ALLOTT, T., EVANS, M., JOOSTEN, H. & STONEMAN, R. (in press). *Peatland Restoration for Ecosystem Services*. IUCN, BES, Cambridge University Press, in press.
- BOYER, M. L. H. & WHEELER, B. D. (1989). Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. *Journal of Ecology* **77**, 597–609.
- BRAGG, O. & LINDSAY, R. (eds) (2003). *Strategy and Action Plan for Mire and Peatland Conservation in Central Europe*. Wetlands International, Wageningen.
- BRANFIREUN, B. A., HEYES, A. & ROULET, N. T. (1996). The hydrology and methylmercury dynamics of a Precambrian Shield headwater peatland. *Water Resources Research* **32**, 1785–1794.
- BRIDGHAM, S. D., PASTOR, J., JANSSENS, J. A., CHAPIN, C. & MALTERER, T. J. (1996). Multiple limiting gradients in peatlands: a call for a new paradigm. *Wetlands* **16**, 45–65.

- BROWN, J., MITCHELL, N. & BERESFORD, M. (2004). *The Protected Landscape Approach: Linking Nature, Culture and Community*. IUCN, Gland, Switzerland and Cambridge.
- BUBIER, J. L. (1995). The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *Journal of Ecology* **83**, 403–420.
- BURGIN, A. J. & HAMILTON, S. K. (2007). Have we overemphasized the role of denitrification in aquatic ecosystems? A review of nitrate removal pathways. *Frontiers in Ecology and the Environment* **5**, 89–96.
- BYRNE, K. A., CHOJNICKI, B., CHRISTENSEN, T. R., DRÖSLER, M., FREIBAUER, A., FRIBORG, T., FROLKING, S., LINDROTH, A., MAILHAMMER, J., MALMER, N., SELIN, P., TURUNEN, J., VALENTINI, R. & ZETTERBERG, L. (2004). EU peatlands: current carbon stocks and trace gas fluxes. In *CarboEurope-GHG Concerted Action – Synthesis of the European Greenhouse Gas Budget*, Report 4/2004 (eds T. R. CHRISTENSEN and T. FRIBORG). Specific Study, Tipo-Lito Recchioni, Viterbo.
- CARACO, N. F., COLE, J. J. & LIKENS, G. E. (1989). Evidence for sulphate-controlled phosphorus release from sediments of aquatic systems. *Nature* **341**, 156–158.
- COBBAERT, D., ROCHEFORT, L. & PRICE, J. S. (2004). Experimental restoration of a fen plant community after peat mining. *Applied Vegetation Science* **7**, 209–220.
- COOKE, G. D., WELCH, E. B., MARTIN, A. B., FULMER, D. G., HYDE, J. B. & SCHRIEVE, G. D. (1993). Effectiveness of Al, Ca, and Fe salts for control of internal phosphorus loading in shallow and deep lakes. *Hydrobiologia* **253**, 323–335.
- COOPER, D. J., MACDONALD, L. H., WENGER, S. K. & WOODS, S. W. (1998). Hydrologic restoration of a fen in Rocky Mountain National Park, Colorado, USA. *Wetlands* **18**, 335–345.
- COSTANZA, R., D'ARGE, R., DE GROOT, R., FARBERK, S., GRASSO, M., HANNON, B., LIMBURG, K., NAEEM, S., O'NEILL, R. V., PARUELO, J., RASKIN, R. G., SUTTON, P. & VAN DEN BELT, M. (1997). The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260.
- CRAFT, C. B., VYMAZAL, J. & RICHARDSON, C. J. (1995). Response of Everglades plant-communities to nitrogen and phosphorus additions. *Wetlands* **15**, 258–271.
- CRABINE, J. M., FIERER, N. & MCLAUCHLAN, K. K. (2010). Widespread coupling between the rate and temperature sensitivity of organic matter decay. *Nature Geoscience* **3**, 854–857.
- CUSELL, C., LAMERS, L. P. M., VAN WIRDUM, G. & KOOLJMAN, A. M. (2013). Impacts of water level fluctuation on mesotrophic rich fens: acidification vs. eutrophication. *Journal of Applied Ecology* **50**, 998–1009 (doi: 10.1111/1365-2664.12096).
- CUSELL, C., KOOLJMAN, A., FERNANDEZ, F., VAN WIRDUM, G., GEURTS, J. J. M., VAN LOON, E. E., KALBITZ, K. & LAMERS, L. P. M. (2014). Filtering fens: mechanisms explaining phosphorus-limited hotspots of biodiversity in wetlands adjacent to heavily fertilized areas. *Science of the Total Environment* **481**, 129–141.
- DE GRAAF, M. C. C., BOBBINK, R., VERBEEK, P. J. M. & ROELOFS, J. G. M. (1997). Aluminium toxicity and tolerance in three heathland species. *Water, Air, & Soil Pollution* **98**, 229–239.
- DE GROOT, R. S., WILSON, M. A. & BOUMANS, R. M. J. (2002). A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics* **41**, 393–408.
- DE VERE, N., JONGEJANS, E., PLOWMAN, A. & WILLIAMS, E. (2009). Population size and habitat quality affect genetic diversity and fitness in the clonal herb *Cirsium dissectum*. *Oecologia* **159**, 59–68.
- DIERBERG, F. E., DEBUSK, T. A., LARSON, N. R., KHARBANDA, M. D., CHAN, N. & GABRIEL, M. C. (2011). Effects of sulfate amendments on mineralization and phosphorus release from South Florida (USA) wetland soils under anaerobic conditions. *Soil Biology and Biochemistry* **43**, 31–45.
- DINGEMANS, B. J. J., BAKKER, E. S. & BODELIER, P. L. E. (2011). Aquatic herbivores facilitate the emission of methane from wetlands. *Ecology* **92**, 1166–1173.
- DREWER, J., LOHILA, A., AURELA, M., LAURILA, T., MINKKINEN, K., PENTTILA, T., DINSMORE, K. J., MCKENZIE, R. M., HELFTER, C., FLECHARD, C., SUTTON, M. A. & SKIBA, U. M. (2010). Comparison of greenhouse gas fluxes and nitrogen budgets from an ombrotrophic bog in Scotland and a minerotrophic sedge fen in Finland. *European Journal of Soil Science* **61**, 640–650.
- EGNÉR, H., RIEHM, H. & DOMINGO, W. R. (1960). Untersuchungen über die chemische Bodenanalyse als Grundlage für die Beurteilung des Nährstoffzustandes der Böden. II. Chemische Extraktionsmethoden zur Phosphor- und Kaliumbestimmung. *Kungliga Lantbruks högskolans Annaler* **26**, 199–215.
- EINSELE, W. & VETTER, H. (1938). Untersuchungen über die Entwicklung der physikalischen und chemischen Verhältnisse im Jahreszyklus in einem mäßig eutrophen See (Schleisssee bei Langenargen). *Internationale Revue der gesamten Hydrobiologie und Hydrographie* **36**, 285–324.
- ELSER, J. J., BRACKEN, M. E. S., CLELAND, E. E., GRUNER, D. S., HARPOLE, W. S., HILLEBRAND, H., NGAL, J. T., SEABLOOM, E. W., SHURIN, J. B. & SMITH, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* **10**, 1135–1142.
- ESTOP-ARAGONES, C. & BLODAU, C. (2012). Effects of experimental drying intensity and duration on respiration and methane production recovery in fen peat incubations. *Soil Biology and Biochemistry* **47**, 1–9.
- EVANS, M. G., BURR, T. B. & ADAMSON, J. K. (1999). Runoff generation and water table fluctuations in blanket peat: evidence from UK data spanning the dry summer of 1995. *Journal of Hydrology* **221**, 141–160.
- FAN, Z., MCGUIRE, A. D., TURETSKY, M. R., HARDEN, J. W., WADDINGTON, J. M. & KANE, E. S. (2013). The response of soil organic carbon of a rich fen peatland in interior Alaska to projected climate change. *Global Change Biology* **19**, 604–620.
- FENNER, N. & FREEMAN, C. (2011). Drought-induced carbon loss in peatlands. *Nature Geoscience* **4**, 895–900.
- FENNER, N., WILLIAMS, R., TOBERMAN, H., HUGHES, S., REYNOLDS, B. & FREEMAN, C. (2011). Decomposition 'hotspots' in a rewetted peatland: implications for water quality and carbon cycling. *Hydrobiologia* **674**, 51–66.
- FISHER, J. & ACREMAN, M. C. (2004). Wetland nutrient removal: a review of the evidence. *Hydrology and Earth System Sciences* **8**, 673–685.
- FOLEY, J. A., DEFRIES, R., ASNER, G. P., BARFORD, C., BONAN, G., CARPENTER, S. R., CHAPIN, F. S., COE, M. T., DAILY, G. C., GIBBS, H. K., HELKOWSKI, J. H., HOLLOWAY, T., HOWARD, E. A., KUCCHARIK, C. J., MONFREDA, C., PATZ, J. A., PRENTICE, I. C., RAMANKUTTY, N. & SNYDER, P. K. (2005). Global consequences of land use. *Science* **309**, 570–574.
- FREEMAN, C., EVANS, C. D., MONTEITH, D. T., REYNOLDS, B. & FENNER, N. (2001a). Export of carbon from peat soils. *Nature* **412**, 785.
- FREEMAN, C., OSTLE, N. & KANG, H. (2001b). An enzymic 'latch' on a global carbon store – a shortage of oxygen locks up carbon in peatlands by restraining a single enzyme. *Nature* **409**, 149.
- FREEMAN, C., FENNER, N. & SHIRSAT, A. H. (2012). Peatland geoengineering: an alternative approach to terrestrial carbon sequestration. *Philosophical Transactions of the Royal Society of London, Series A: Mathematical, Physical and Engineering Sciences* **370**, 4404–4421.
- FREEMAN, C., LOCK, M. A. & REYNOLDS, B. (1993). Fluxes of CO₂, CH₄, and N₂O from a Welsh peatland following simulation of water table draw-down: potential feedback to climatic change. *Biogeochemistry* **19**, 51–60.
- FREIBAUER, A., ROUNSEVELL, M. D. A., SMITH, P. & VERHAGEN, J. (2004). Carbon sequestration in the agricultural soils of Europe. *Geoderma* **122**, 1–23.
- GALLOWAY, J. N., DENTENER, F. J., CAPONE, D. G., BOYER, E. W., HOWARTH, R. W., SEITZINGER, S. P., ASNER, G. P., CLEVELAND, C. C., GREEN, P. A., HOLLAND, E. A., KARL, D. M., MICHAELS, A. F., PORTER, J. H., TOWNSEND, A. R. & VÖOSMARTY, C. J. (2004). Nitrogen cycles: past, present, and future. *Biogeochemistry* **70**, 153–226.
- GAUCI, V., MATTHEWS, E., DISE, N., WALTER, B., KOCH, D., GRANBERG, G. & VILE, M. A. (2004). Sulfur pollution suppression of the wetland methane source in the 20th and 21st centuries. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 12583–12587.
- GEURTS, J. J. M., SMOLDERS, A. J. P., VERHOEVEN, J. T. A., ROELOFS, J. G. M. & LAMERS, L. P. M. (2008). Sediment Fe:PO₄ ratio as a diagnostic and prognostic tool for the restoration of macrophyte biodiversity in fen waters. *Freshwater Biology* **53**, 2101–2116.
- GEURTS, J. J. M., VAN DE WOUW, P. A. G., SMOLDERS, A. J. P., ROELOFS, J. G. M. & LAMERS, L. P. M. (2011). Ecological restoration on former agricultural soils: feasibility of in situ phosphate fixation as an alternative to top soil removal. *Ecological Engineering* **37**, 1620–1629.
- GIGNAC, L. D., GAUTHIER, R., ROCHEFORT, L. & BUBIER, J. (2004). Distribution and habitat niches of 37 peatland Cyperaceae species across a broad geographic range in Canada. *Canadian Journal of Botany* **82**, 1292–1313.
- GOLTERMAN, H. L. (2001). Phosphate release from anoxic sediments or 'What did Mortimer really write?'. *Hydrobiologia* **450**, 99–106.
- GORE, A. J. P. (ed.) (1983). *Mires – Swamp, Bog, Fen and Moor. Ecosystems of the World*, 4A. Elsevier, Amsterdam.
- GORHAM, E. (1991). Northern peatlands – role in the carbon-cycle and probable responses to climatic warming. *Ecological Applications* **1**, 182–195.
- GORHAM, E. (1995). The biogeochemistry of northern peatlands and its possible responses to global warming. In *Biotic Feedbacks in the Global Climatic System: Will the Warming Feed the Warming?* (eds G. M. WOODWELL and F. T. MACKENZIE), pp. 169–187. Oxford University Press, New York.
- GORHAM, E., BAYLEY, S. E. & SCHINDLER, D. W. (1984). Ecological effects of acid deposition upon peatlands – a neglected field in acid-rain research. *Canadian Journal of Fisheries and Aquatic Sciences* **41**, 1256–1268.
- GRAF, M. D., BÉRUBÉ, V. & ROCHEFORT, L. (2012). Restoration of peatlands after peat extraction: impacts, restoration goals and techniques. In *Restoration and Reclamation of Boreal Ecosystems* (eds D. H. VITT and J. BHATTI), pp. 259–280. Cambridge University Press, Cambridge.
- GRAF, M. D. & ROCHEFORT, L. (2008). Techniques for restoring fen vegetation on cut-away peatlands in North America. *Applied Vegetation Science* **11**, 521–528.
- GRAF, M. D. & ROCHEFORT, L. (2009). Examining the peat-accumulating potential of fen vegetation in the context of fen restoration of harvested peatlands. *Ecoscience* **16**, 158–166.
- GRAF, M. D. & ROCHEFORT, L. (2010). Moss regeneration for fen restoration: field and greenhouse experiments. *Restoration Ecology* **18**, 121–130.
- GRIME, J. P. (1974). Vegetation classification by reference to strategies. *Nature* **250**, 26–31.
- GROOTJANS, A. P., ADEMA, E. B., BLEUTEN, W., JOOSTEN, H., MADARAS, M. & JANAKOVA, M. (2006). Hydrological landscape settings of base-rich fen mires and fen meadows: an overview. *Applied Vegetation Science* **9**, 175–184.

- GROOTJANS, A. P. & VAN DIGGELEN, R. (1995). Assessing the restoration prospects of degraded fens. In *Restoration of Temperate Wetlands* (eds B. D. WHEELER, S. C. SHAW, W. J. FOJ and R. A. ROBERTSON), pp. 73–90. John Wiley & Sons, Ltd, Chichester.
- GROOTJANS, A. P., VAN DIGGELEN, R., WASSEN, M. J. & WIERSINGA, W. A. (1988). The effects of drainage on groundwater quality and plant-species distribution in stream valley meadows. *Vegetatio* **75**, 37–48.
- GUNNARSON, U., RYDIN, H. & SJÖRS, H. (2000). Diversity and pH changes after 50 years on the boreal mire Skatllöbergs Stormosse, central Sweden. *Journal of Vegetation Science* **11**, 277–286.
- GÜSEWELL, S. (2004). N:P ratios in terrestrial plants: variation and functional significance. *New Phytologist* **164**, 243–266.
- HARPER, J. L. (1977). *Population Biology of Plants*. Academic Press, London.
- HAUTIER, Y., NIKLAUS, P. A. & HECTOR, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science* **324**, 636–638.
- HECKY, R. E. & KILHAM, P. (1988). Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnology and Oceanography* **33**, 796–822.
- HENDRIKS, D. M. D., VAN HUISTEDEN, J., DOLMAN, A. J. & VAN DER MOLEN, M. K. (2007). The full greenhouse gas balance of an abandoned peat meadow. *Biogeosciences* **4**, 411–424.
- HEIN, L., VAN KOPPEN, K., DE GROOT, R. S. & VAN IERLAND, E. C. (2006). Spatial scales, stakeholders and the valuation of ecosystem services. *Ecological Economics* **57**, 209–228.
- HOBBS, R. J. & NORTON, D. A. (1996). Towards a conceptual framework for restoration ecology. *Restoration Ecology* **4**, 93–110.
- HOLDEN, J., GASCOIGN, M. & BOSANKO, N. R. (2007). Erosion and natural revegetation associated with surface land drains in upland peatlands. *Earth Surface Processes and Landforms* **32**, 1547–1557.
- ISE, T., DUNN, A. L., WOFESY, S. C. & MOORCROFT, P. R. (2008). High sensitivity of peat decomposition to climate change through water-table feedback. *Nature Geoscience* **1**, 763–766.
- JACOBS, C. M. J., JACOBS, A. F. G., BOSVELD, F. C., HENDRIKS, D. M. D., HENSEN, A., KROON, P. S., MOORS, E. J., NOL, L., SCHRIER-UIJL, A. & VEENENDAAL, E. M. (2007). Variability of annual CO₂ exchange from Dutch grasslands. *Biogeosciences* **4**, 803–816.
- JNCC (2011). Towards an assessment of the state of UK Peatlands. Joint Nature Conservation Committee Report No. 445. JNCC, Peterborough.
- JOOSTEN, H. & CLARKE, D. (2002). *Wise Use of Peatlands*. International Mire Conservation Group and International Peat Society, Jyväskylä.
- KALBITZ, K., SOLINGER, S., PARK, J. H., MICHALZIK, B. & MATZNER, E. (2000). Controls on the dynamics of dissolved organic matter in soils: a review. *Soil Science* **165**, 277–304.
- KANG, H., FREEMAN, C. & LOCK, M. A. (1998). Trace gas emissions from a north Wales fen – role of hydrochemistry and soil enzyme activity. *Water, Air, & Soil Pollution* **105**, 107–116.
- KASIMIR-KLEMEDTSSON, A., KLEMEDTSSON, L., BERGLUND, K., MARTIKAINEN, P., SILVOLA, J. & OENEMA, O. (1997). Greenhouse gas emissions from farmed organic soils: a review. *Soil Use and Management* **13**, 245–250.
- KIEHL, K., KIRMER, A., DONATH, T. W., RASRAN, L. & HÖLZEL, N. (2010). Species introduction in restoration projects – evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic and Applied Ecology* **11**, 285–299.
- KIRSCHBAUM, M. U. F. (2000). Forest growth and species distribution in a changing climate. *Tree Physiology* **20**, 309–322.
- KLEIJN, D., BAQUERO, R. A., CLOUGH, Y., DIAZ, M., DE ESTEBAN, J., FERNANDEZ, F., GABRIEL, D., HERZOG, F., HOLZSCHUH, A., JOHL, R., KNOP, E., KRUESS, A., MARSHALL, E. J. P., STEFFAN-DEWENTER, I., TSCHARNTKE, T., VERHULST, J., WEST, T. M. & YELA, J. L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters* **9**, 243–254.
- KLIMKOWSKA, A., GROOTJANS, A. P., KOTOWSKI, W. & VAN DIGGELEN, R. (2010). Prospects for fen meadow restoration on severely degraded fens. *Perspectives in Plant Ecology, Evolution and Systematics* **12**, 245–255.
- KLIMKOWSKA, A., VAN DIGGELEN, R., BAKKER, J. P. & GROOTJANS, A. P. (2007). Wet meadow restoration in Western Europe: a quantitative assessment of the effectiveness of several techniques. *Biological Conservation* **140**, 318–328.
- KOCH, M. S., MENDELSSOHN, I. A. & MCKEE, K. L. (1990). Mechanism for the sulfide-induced growth limitation in wetland macrophytes. *Limnology and Oceanography* **35**, 399–408.
- KOERSELMAN, W., BAKKER, S. A. & BLOM, M. (1990). Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. *Journal of Ecology* **78**, 428–442.
- KOERSELMAN, W. & MEULEMAN, A. F. M. (1996). The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *Journal of Applied Ecology* **33**, 1441–1450.
- KOOIJMAN, A. M. (2012). 'Poor rich fen mosses': atmospheric N-deposition and P-eutrophication in base-rich fens. *Lindbergia* **35**, 42–52.
- KOOIJMAN, A. M. & BAKKER, C. (1995). Species replacement in the bryophyte layer in mires: the role of water type, nutrient supply and interspecific interactions. *Journal of Ecology* **83**, 1–8.
- KOOIJMAN, A. M., BELTMAN, B. & WESTHOFF, V. (1994). Extinction and reintroduction of the bryophyte *Scorpidium scorpioides* in a rich-fen spring site in the Netherlands. *Biological Conservation* **69**, 87–96.
- KOOIJMAN, A. M. & HEDENÄS, L. (2009). Changes in nutrient availability from calcareous to acid wetland habitats with closely related brownmoss species: increase instead of decrease in N and P. *Plant and Soil* **324**, 267–278.
- KOOIJMAN, A. M. & PAULISSEN, M. P. C. P. (2006). Higher acidification rates in fens with phosphorus enrichment. *Applied Vegetation Science* **9**, 205–212.
- KOTOWSKI, W. & VAN DIGGELEN, R. (2004). Light as an environmental filter in fen vegetation. *Journal of Vegetation Science* **15**, 583–594.
- LAMERS, L. P. M. (2001). Tackling biogeochemical questions in peatlands. PhD Thesis: University of Nijmegen. http://webdoc.uibn.kun.nl/mono/1/lamers_1/index.html Accessed 1.12.2013.
- LAMERS, L. P. M., FALLA, S.-J., SAMBORSKA, E. M., VAN DULKEN, I. A. R., VAN HENGSTUM, G. & ROELOFS, J. G. M. (2002a). Factors controlling the extent of eutrophication and toxicity in sulfate-polluted freshwater wetlands. *Limnology and Oceanography* **47**, 585–593.
- LAMERS, L. P. M., SMOLDERS, A. J. P. & ROELOFS, J. G. M. (2002b). The restoration of fens in the Netherlands. In *The Ecological Restoration of Wetlands in the Netherlands* (eds P. H. NIENHUIS and R. GULATI), pp. 107–130. Kluwer Academic Publishers, Amsterdam. Also in *Hydrobiologia*, **478**.
- LAMERS, L. P. M., GOVERS, L. L., JANSSEN, I. C. J. M., GEURTS, J. G. M., VAN DER WELLE, M. E. W., VAN KATWIJK, M. M., VAN DER HEIDE, T., ROELOFS, J. G. M. & SMOLDERS, A. J. P. (2013). Sulfide as a soil phytotoxin – a review. *Frontiers in Plant Science* **4**, 268 (doi: 10.3389/fpls.2013.00268).
- LAMERS, L. P. M., LOEB, R., ANTHEUNISSE, A. M., MILETTO, M., LUCASSEN, E. C. H. E. T., BOXMAN, A. W., SMOLDERS, A. J. P. & ROELOFS, J. G. M. (2006). Biogeochemical constraints on the ecological rehabilitation of wetland vegetation in river floodplains. *Hydrobiologia* **565**, 165–186.
- LAMERS, L. P. M., TEN DOLLE, G. E., VAN DEN BERG, S. T. G., VAN DELFT, S. P. J. & ROELOFS, J. G. M. (2001). Differential responses of freshwater wetland soils to sulphate pollution. *Biogeochemistry* **55**, 87–102.
- LAMERS, L. P. M., TOMASSEN, H. B. M. & ROELOFS, J. G. M. (1998a). Sulfate-induced eutrophication and phytotoxicity in freshwater wetlands. *Environmental Science and Technology* **32**, 199–205.
- LAMERS, L. P. M., VAN ROOZENDAAL, S. M. E. & ROELOFS, J. G. M. (1998b). Acidification of freshwater wetlands: combined effects of non-airborne sulfur pollution and desiccation. *Water, Air, & Soil Pollution* **105**, 95–106.
- LAMERS, L. P. M., VAN DIGGELEN, J. M. H., OP DEN CAMP, H. J. M., VISSER, E. J. W., LUCASSEN, E. C. H. E. T., VILE, M. A., JETTEN, M. S. M., SMOLDERS, A. J. P. & ROELOFS, J. G. M. (2012). Microbial transformations of nitrogen, sulfur and iron dictate vegetation composition in wetlands: a review. *Frontiers in Microbiology* **3**, 156.
- LIMPENS, J., BERENDSE, F., BLODAU, C., CANADELL, J. G., FREEMAN, C., HOLDEN, J., ROULET, N., RYDIN, H. & SCHAEPMAN-STRUB, G. (2008). Peatlands and the carbon cycle: from local processes to global implications – a synthesis. *Biogeosciences* **5**, 1475–1491.
- LOEB, R., LAMERS, L. P. M. & ROELOFS, J. G. M. (2008). Prediction of phosphorus mobilisation in inundated floodplain soils. *Environmental Pollution* **156**, 325–331.
- LUCASSEN, E. C. H. E. T., SMOLDERS, A. J. P., LAMERS, L. P. M. & ROELOFS, J. G. M. (2005). Water table fluctuations and groundwater supply are important in preventing phosphate-eutrophication in sulphate-rich fens: consequences for wetland restoration. *Plant and Soil* **269**, 109–115.
- MAHMOOD, M. S. & STRACK, M. (2011). Methane dynamics of recolonized cutover minerotrophic peatland: implications for restoration. *Ecological Engineering* **37**, 1859–1868.
- MALSON, K. & RYDIN, H. (2007). The regeneration capabilities of bryophytes for rich fen restoration. *Biological Conservation* **135**, 435–442.
- MATSON, P. A., PARTON, W. J., POWER, A. G. & SWIFT, M. J. (1997). Agricultural intensification and ecosystem properties. *Science* **277**, 504–509.
- MAURER, D. A. & ZEDLER, J. B. (2002). Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and clonal growth. *Oecologia* **131**, 279–288.
- METTROP, I. S., CUSELLI, C., KOOIJMAN, A. M. & LAMERS, L. P. M. (2014). Nutrient and carbon dynamics in peat from rich fens and *Sphagnum*-fens during different gradations of drought. *Soil Biology and Biochemistry* **68**, 317–328.
- MICHELSEN, B., LAMERS, L. & SMOLDERS, F. (2007). Interne eutrofiëring van veenplassen belangrijker dan voorheen erkend? *H2O* **8**, 51–54 (In Dutch).
- MIDDLETON, B., GROOTJANS, A. P., JENSEN, K., OLDE VENTERINK, H. & KATALIN MARGÓCZI, K. (2006). Fen management and research perspectives: an overview. *Ecological Studies* **191**, 247–268.
- Millennium Ecosystem Assessment (2005). *Ecosystems and Human Well-Being: Wetlands and Water Synthesis*. World Resources Institute, Washington.
- MINAYEVA, T., SIRIN, A. & BRAGG, O. (eds) (2009). *A Quick Scan of Peatlands in Central and Eastern Europe*. Wetlands International, Wageningen.
- MITTSCH, W. J. & GOSSELINK, J. G. (2007). *Wetlands*. Fourth Edition. Van Nostrand Reinhold, New York.
- MOORE, T. R. (1989). Plant production, decomposition and carbon efflux in a subarctic patterned fen. *Arctic and Alpine Research* **21**, 156–162.

- MOORE, P. D. & BELLAMY, W. J. (1974). *Peatlands*. Elek Science, London.
- MOORE, T. R., BUBIER, J. L., FROLKING, S. E., LAFLEUR, P. M. & ROULET, N. T. (2002). Plant biomass and production and CO₂ exchange in an ombrotrophic bog. *Journal of Ecology* **90**, 25–36.
- MOORE, T. R., BUBIER, J. L. & BLEZKI, L. (2007). Litter decomposition in temperate peatland ecosystems: the effect of substrate and site. *Ecosystems* **10**, 949–963.
- MOORMAN, T. B., COWAN, J. K., ARTHUR, E. L. & COATS, J. R. (2001). Organic amendments to enhance herbicide biodegradation in contaminated soils. *Biology and Fertility of Soils* **33**, 541–545.
- NOVAK, J. M. & CHAN, A. S. L. (2002). Development of P-hyperaccumulator plant strategies to remediate soils with excess P concentrations. *Critical Reviews in Plant Sciences* **21**, 493–509.
- NYKÄNEN, H., ALM, J., LÄNG, K., SILVOLA, J. & MARTIKAINEN, P. J. (1995). Emissions of CH₄, N₂O and CO₂ from a virgin fen and a fen drained for grassland in Finland. *Journal of Biogeography* **22**, 351–357.
- OLSEN, S. R., COLE, C. V., WATANABE, F. S. & DEAN, L. A. (1954). *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*, USDA Circular No. 939. U.S. Government Printing Office, Washington.
- OREM, W., GILMOUR, C., AXELRAD, D., KRABENHOFT, D., SCHEIDT, D., KALLA, P., MCCORMICK, P., GABRIEL, M. & AIKEN, G. (2011). Sulfur in the South Florida ecosystem: distribution, sources, biogeochemistry, impacts, and management for restoration. *Critical Reviews in Environmental Science and Technology* **41**, 249–288.
- OUBORG, N. J., VERGEER, P. & MIX, C. (2006). The rough edges of the conservation genetics paradigm for plants. *Journal of Ecology* **94**, 1233–1248.
- PARISH, F., SIRIN, A., CHARMAN, D., JOOSTEN, H., MINAYEVA, T., SILVIUS, M. & STRINGER, L. (eds) (2008). *Assessment on Peatlands, Biodiversity and Climate Change: Main Report*. Global Environment Centre, Kuala Lumpur, Malaysia, and Wetlands International, Wageningen.
- PATZELT, A., WILD, U. & PFADENHAUER, J. (2001). Restoration of wet fen meadows by topsoil removal: vegetation development and germination biology of fen species. *Restoration Ecology* **9**, 127–136.
- PAULISSEN, M. P. C. P., VAN DER VEN, P. J. M., DEES, A. J. & BOBBINK, R. (2004). Differential effects of nitrate and ammonium on three fen bryophyte species in relation to pollutant nitrogen input. *New Phytologist* **164**, 451–458.
- PFADENHAUER, J. & KLÖTZLI, F. (1996). Restoration experiments in middle European wet terrestrial ecosystems: an overview. *Vegetatio* **126**, 101–115.
- PONNAMPERUMA, F. N. (1984). Effects of flooding on soils. In *Flooding and Plant Growth* (ed. T. T. KOZLOWSKI), pp. 10–45. Academic Press, Orlando.
- PORTNOY, S. & WILLSON, M. F. (1993). Seed dispersal curves – behavior of the tail of the distribution. *Evolutionary Ecology* **7**, 25–44.
- Ramsar Convention Secretariat (2013). *The Ramsar Convention Manual: A Guide to the Convention on Wetlands (Ramsar, Iran, 1971)*. Sixth Edition. Ramsar Convention Secretariat, Gland.
- REDDY, K. R., KADLEC, R. H., FLAIG, E. & GALE, P. M. (1999). Phosphorus retention in streams and wetlands: a review. *Critical Reviews in Environmental Science and Technology* **29**, 83–146.
- REDDY, K. R. & RAO, P. S. C. (1983). Nitrogen and phosphorus fluxes from a flooded organic soil. *Soil Science* **136**, 300–307.
- REJMÁNKOVÁ, E. & HOUĐKOVÁ, K. (2006). Wetland plant decomposition under different nutrient conditions: what is more important, litter quality or site quality? *Biogeochemistry* **80**, 245–262.
- REMANE, A. (1934). Die Brackwasserfauna. *Verhandlungen der Deutschen Zoologischen Gesellschaft* **36**, 34–74.
- RICHARDSON, C. J. (1985). Mechanisms controlling phosphorus retention capacity in freshwater wetlands. *Science* **228**, 1424–1427.
- RICHARDSON, C. J. (1994). Ecological functions and human-values in wetlands – a framework for assessing forestry impacts. *Wetlands* **14**, 1–9.
- RICHARDSON, C. J. (2008). *The Everglades Experiments: Lessons for Ecosystem Restoration*. Springer-Verlag, New York.
- RICHARDSON, C. J. (2010). The Everglades: North America's subtropical wetland. *Wetlands Ecology and Management* **18**, 517–542.
- RICHARDSON, C. J., FLANAGAN, N. E., HO, M. C. & PAHL, J. W. (2011). Integrated stream and wetland restoration: a watershed approach to improved water quality on the landscape. *Ecological Engineering* **37**, 25–39.
- RICHARDSON, C. J. & HUSSAIN, N. A. (2006). Restoring the Garden of Eden. An ecological assessment of the marshes of Iraq. *Bioscience* **56**, 477–489.
- RICHARDSON, C. J. & MARSHALL, P. E. (1986). Processes controlling movement, storage and export of phosphorus in a fen peatland. *Ecological Monographs* **56**, 279–302.
- ROCHFORT, L. (in press). Restoration of peatlands after industrial activities. In *Peatland Restoration for Ecosystem Services* (eds A. BONN, T. ALLOTT, M. EVANS, H. JOOSTEN and R. STONEMAN). IUCN, BES, Cambridge University Press, in press.
- ROELOFS, J. G. M. (1991). Inlet of alkaline river water into peaty lowlands: effects on water quality and *Stratiotes aloides* L. stands. *Aquatic Botany* **39**, 267–293.
- ROULET, N. (2000). Peatlands, carbon storage, greenhouse gases, and the Kyoto Protocol: prospects and significance for Canada. *Wetlands* **20**, 605–615.
- SAARINEN, T. (1996). Biomass and production of two vascular plants in a boreal mesotrophic fen. *Canadian Journal of Botany* **74**, 934–938.
- SARNEEL, J. M., GEURTS, J. J. M., BELTMAN, B., LAMERS, L. P. M., NIJZINK, M. M., SOONS, M. B. & VERHOEVEN, J. T. A. (2010). The effect of nutrient enrichment of either the bank or the surface water on shoreline vegetation and decomposition. *Ecosystems* **13**, 1275–1286.
- SARNEEL, J. M., SOONS, M. B., GEURTS, J. J. M., BELTMAN, B. & VERHOEVEN, J. T. A. (2011). Multiple effects of land-use changes impede the colonization of open water in fen ponds. *Journal of Vegetation Science* **22**, 551–563.
- SAUNDERS, D. A., HOBBS, R. J. & MARGULES, C. R. (1991). Biological consequences of ecosystem fragmentation – a review. *Conservation Biology* **5**, 18–32.
- SCHINDLER, D. W. (2000). Evolution of phosphorus limitation in lakes. *Science* **195**, 260–262.
- SCHLESINGER, W. H. & ANDREWS, J. A. (2000). Soil respiration and the global carbon cycle. *Biogeochemistry* **48**, 7–20.
- SCHRAUTZER, J., ASSHOFF, M. & MULLER, F. (1996). Restoration strategies for wet grasslands in Northern Germany. *Ecological Engineering* **7**, 255–278.
- SMITH, L. M., EULLIS, N. H., WILCOX, D. A. & BRINSON, M. M. (2008). Application of a geomorphic and temporal perspective to wetland management in North America. *Wetlands* **28**, 563–577.
- SMOLDERS, A. J. P., LAMERS, L. P. M., LUCASSEN, E. C. H. E. T., VAN DER VELDE, G. & ROELOFS, J. G. M. (2006). Internal eutrophication: 'how it works and what to do about it', a review. *Chemistry and Ecology* **22**, 93–111.
- SMOLDERS, A. J. P., LUCASSEN, E. C. H. E. T., BOBBINK, R., ROELOFS, J. G. M. & LAMERS, L. P. M. (2010). How nitrate leaching from agricultural lands provokes phosphate eutrophication in groundwater fed wetlands: the sulphur bridge. *Biogeochemistry* **98**, 1–7.
- SMOLDERS, A. J. P., LUCASSEN, E. C. H. E. T., VAN DER AALST, M., LAMERS, L. P. M. & ROELOFS, J. G. M. (2008). Decreasing the abundance of *Juncus effusus* on former agricultural lands with noncalcareous sandy soils: possible effects of liming and soil removal. *Restoration Ecology* **16**, 240–248.
- SMOLDERS, A. J. P., NIJBOER, R. C. & ROELOFS, J. G. M. (1995). Prevention of sulphide accumulation and phosphate mobilization by the addition of iron(II) chloride to a reduced sediment: an enclosure experiment. *Freshwater Biology* **34**, 559–568.
- SMOLDERS, A. J. P. & ROELOFS, J. G. M. (1996). The roles of internal iron hydroxide precipitation, sulphide toxicity and oxidizing ability in the survival of *Stratiotes aloides* roots at different iron concentrations in sediment pore water. *New Phytologist* **133**, 253–260.
- SMOLDERS, A. J. P., TOMASSEN, H. B. M., PIJNAPPEL, H. W., LAMERS, L. P. M. & ROELOFS, J. G. M. (2001). Substrate-derived CO₂ is important in the development of *Sphagnum* spp. *New Phytologist* **152**, 325–332.
- SOLOMON, K. R., BAKER, D. B., RICHARDS, R. P., DIXON, D. R., KLAINE, S. J., LAPOINT, T. W., KENDALL, R. J., WEISSKOPF, C. P., GIDDINGS, J. M., GIESY, J. P., HALL, L. W. & WILLIAMS, W. M. (1996). Ecological risk assessment of atrazine in North American surface waters. *Environmental Toxicology and Chemistry* **15**, 31–74.
- SOLOMON, S., QIN, D., MANNING, M., CHEN, Z., MARQUIS, M., AVERYT, K. B., TIGNOR, M. & MILLER, H. L. (eds) (2007). *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, and New York.
- SOONS, M. B., HEIL, G. W., NATHAN, R. & KATUL, G. G. (2004). Determinants of long-distance seed dispersal by wind in grasslands. *Ecology* **85**, 3056–3068.
- SOONS, M. B., MESSELINK, J. H., JONGEJANS, E. & HEIL, G. W. (2005). Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. *Journal of Ecology* **93**, 1214–1225.
- SORENSEN, A. E. (1986). Seed dispersal by adhesion. *Annual Review of Ecology and Systematics* **17**, 443–463.
- STEVENS, C. J., MANNING, P., VAN DEN BERG, L. J. L., DE GRAAF, M. C. C., WAMELINK, G. W. W., BOXMAN, A. W., BLEEKER, A., VERGEER, P., ARRONIZ-CRESPO, M., LIMPENS, J., LAMERS, L. P. M., BOBBINK, R. & DORLAND, E. (2011). Ecosystem responses to reduced and oxidised nitrogen inputs in European terrestrial habitats. *Environmental Pollution* **159**, 665–676.
- STRACK, M. (ed.) (2008). *Peatlands and Climate Change*. IPCC, Finland.
- STRAKOVA, P., NIEMI, R. M., FREEMAN, C., PELTONIEMI, K., TOBERMAN, H., HEISKANEN, I., FRITZE, H. & LAIHO, R. (2011). Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water regimes. *Biogeosciences* **8**, 2741–2755 (doi: 10.5194/BG-8-2741-2011).
- STRYKSTRA, R. J., BEKKER, R. M. & BAKKER, J. P. (1998). Assessment of dispersule availability: its practical use in restoration management. *Acta Botanica Neerlandica* **47**, 57–70.
- STRYKSTRA, R. J., VERWEIJ, G. L. & BAKKER, J. P. (1997). Seed dispersal by mowing machinery in a Dutch brook valley system. *Acta Botanica Neerlandica* **46**, 387–401.
- TARNOCAI, C., KETTLES, I. M. & LACELLE, B. (2000). *Peatlands of Canada Digital Database*. Geological Survey of Canada, Ottawa, Open File 3834.
- TER HEERDT, G. N. J., SCHUTTER, A. & BAKKER, J. P. (1999). The effect of water supply on seed-bank analysis using the seedling-emergence method. *Functional Ecology* **13**, 428–430.
- THOMPSON, K., BAKKER, J. P. & BEKKER, R. M. (1997). *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*. Cambridge University Press, Cambridge.

- THURSTON, R. V., RUSSO, R. C. & VINOGRADOV, R. V. (1981). Ammonia toxicity to fishes – effect of pH on the toxicity of the un-ionized ammonia species. *Environmental Science & Technology* **15**, 837–840.
- TURUNEN, J. (2008). Development of Finnish peatland area and carbon storage 1950–2000. *Boreal Environment Research* **13**, 319–334.
- VAN DEN BERG, L. J. L., DORLAND, E., VERGEER, P., HART, M. A. C., BOBBINK, R. & ROELOFS, J. G. M. (2005). Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity in combination with low pH. *New Phytologist* **166**, 551–564.
- VAN DEN BROEK, T., VAN DIGGELEN, R. & BOBBINK, R. (2005). Variation in seed buoyancy of species in wetland ecosystems with different flooding dynamics. *Journal of Vegetation Science* **16**, 579–586.
- VAN DER WELLE, M. E. W., CUPPENS, M. L. C., LAMERS, L. P. M. & ROELOFS, J. G. M. (2006). Detoxifying toxicants: interactions between iron and sulfide toxicity in freshwater wetlands. *Environmental Toxicology and Chemistry* **25**, 1592–1597.
- VAN DIGGELEN, R., GROOTJANS, A. P. & HARRIS, J. A. (2001). Ecological restoration: state of the art or state of the science. *Restoration Ecology* **9**, 115–118.
- VAN DIGGELEN, R., MOLENAAR, W. J. & KOIJMAN, A. M. (1996). Vegetation succession in a floating mire in relation to management and hydrology. *Journal of Vegetation Science* **7**, 809–820.
- VAN DIJK, J., STROETENGA, M., BOS, L., VAN BODEGOM, P. M., VERHOEF, H. A. & AERTS, R. (2004). Restoring natural seepage conditions on former agricultural grasslands does not lead to reduction of organic matter decomposition and soil nutrient dynamics. *Biogeochemistry* **71**, 317–337.
- VAN DIJK, J., STROETENGA, M., VAN BODEGOM, P. M. & AERTS, R. (2007). The contribution of rewetting to vegetation restoration of degraded peat meadows. *Applied Vegetation Science* **10**, 315–324.
- VAN GROENENDAEL, J. M., OUBORG, N. J. & HENDRIKS, R. J. J. (1998). Criteria for the introduction of plant species. *Acta Botanica Neerlandica* **47**, 3–13.
- VAN WIRDUM, G., DEN HELD, A. J. & SCHMITZ, M. (1992). Terrestrializing fen vegetation in former turbaries in the Netherlands. In *Fens and Bogs in the Netherlands: Vegetation, History, Nutrient Dynamics and Conservation* (ed. J. T. A. VERHOEVEN), pp. 323–360. Kluwer Academic Publishers, Dordrecht.
- VENTERINK, H. O., WASSEN, M. J., VERKROOST, A. W. M. & DE RUITER, P. C. (2003). Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. *Ecology* **84**, 2191–2199.
- VERBERK, W. C. E. P., LEUVEN, R. S. E. W., VAN DUINEN, G. A. & ESSELINK, H. (2010). Loss of environmental heterogeneity and aquatic macroinvertebrate diversity following large-scale restoration management. *Basic and Applied Ecology* **11**, 440–449.
- VERGEER, P., RENGELINK, R., COPAL, A. & OUBORG, N. J. (2003). The interacting effects of genetic variation, habitat quality and population size on performance of *Succisa pratensis*. *Journal of Ecology* **91**, 18–26.
- VERHOEVEN, J. T. A., ARHEIMER, B., YIN, C. Q. & HEFTING, M. M. (2006). Regional and global concerns over wetlands and water quality. *Trends in Ecology & Evolution* **21**, 96–103.
- VERHOEVEN, J. T. A., BELTMAN, B., DORLAND, E., ROBAT, S. A. & BOBBINK, R. (2011). Differential effects of ammonium and nitrate deposition on fen phanerogams and bryophytes. *Applied Vegetation Science* **14**, 149–157.
- VERHOEVEN, J. T. A., KOERSELMAN, W. & MEULEMAN, A. F. M. (1996). Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. *Trends in Ecology & Evolution* **11**, 494–497.
- VERHOEVEN, J. T. A., MALTBY, E. & SCHMITZ, M. B. (1990). Nitrogen and phosphorus mineralization in fens and bogs. *Journal of Ecology* **78**, 713–726.
- VERHOEVEN, J. T. A. & SETTER, T. L. (2010). Agricultural use of wetlands: opportunities and limitations. *Annals of Botany* **105**, 155–163.
- VICKERY, J. A., TALLOWIN, J. R., FEBER, R. E., ASTERAKI, E. J., ATKINSON, P. W., FULLER, R. J. & BROWN, V. K. (2001). The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* **38**, 647–664.
- VILE, M. A., BRIDGHAM, S. D., WIEDER, R. K. & NOVAK, M. (2003). Atmospheric sulfur deposition alters pathways of gaseous carbon production in peatlands. *Global Biogeochemical Cycles* **17** (doi: 10.1029/2002GB001966).
- VILE, M. A., SCOTT, K. D., BRAULT, E., WIEDER, R. K. & VITT, D. H. (2011). Living on the edge: the effects of drought on Canada's western boreal peatlands. In *Bryophyte Ecology and Climate Change* (eds Z. TUBA, N. G. SLACK and L. R. STARK), pp. 277–298. Cambridge University Press, Cambridge and New York.
- VITT, D. H. & BHATTI, J. (eds) (2012). *Restoration and Reclamation of Boreal Ecosystems*. Cambridge University Press, Cambridge and New York.
- VITT, D. H., WIEDER, R. K., SCOTT, K. D. & FALLER, S. (2009). Decomposition and peat accumulation in rich fens of Boreal Alberta, Canada. *Ecosystems* **12**, 360–373.
- VITT, D. H., WIEDER, R. K., XU, B., KASKIE, M. & KOROPCHAK, S. (2011). Peatland establishment on mineral soils: effects of water level, amendments, and species after two growing seasons. *Ecological Engineering* **37**, 354–363.
- VITOUSEK, P. M. & HOWART, R. W. (1991). Nitrogen limitation on land and in the sea – how can it occur. *Biogeochemistry* **13**, 87–115.
- VON LIEBIG, J. (1843). *Die Chemie in ihrer Anwendung auf Agricultur und Physiologie*. Verlag von Friedrich und Sohn, Braunschweig, Prussia.
- VOS, J. G., DYBING, E., GREIM, H. A., LADEFEGED, O., LAMBRE, C., TARAZONA, J. V., BRANDT, I. & VETHAAK, A. D. (2000). Health effects of endocrine-disrupting chemicals on wildlife, with special reference to the European situation. *Critical Reviews in Toxicology* **30**, 71–133.
- VYMAZAL, J. (2007). Removal of nutrients in various types of constructed wetlands. *Science of the Total Environment* **380**, 48–65.
- WADDINGTON, J. M. & DAY, S. M. (2007). Methane emissions from a peatland following restoration. *Journal of Geophysical Research* **112**, G03018 (doi: 10.1029/2007JG000400).
- WASSEN, M. J., VENTERINK, H. O., LAPSHINA, E. D. & TANNEBERGER, F. (2005). Endangered plants persist under phosphorus limitation. *Nature* **437**, 547–550.
- WAUGHMAN, G. J. (1980). Chemical aspects of some South German Peatlands. *Journal of Ecology* **68**, 1025–1046.
- WHEELER, B. D., GOWING, D. J. G., SHAW, S. C., MOUNTFORD, J. O. & MONEY, R. P. (2004). *Eco-Hydrological Guidelines for Lowland Wetland Plant Communities*. Environment Agency, Bristol.
- WHEELER, B. D. & PROCTOR, M. C. F. (2000). Ecological gradients, subdivisions and terminology of north-west European mires. *Journal of Ecology* **88**, 187–203.
- WHEELER, B. D. & SHAW, S. C. (1995). *Restoration of Damaged Peatlands, with Particular Reference to Lowland Raised Bogs Affected by Peat Extraction*. HMSO, London.
- WHITEMAN, M., JOSÉ, P., GROUT, M., BROOKS, A., QUINN, S. & ACREMAN, M. C. (2004). Local impact assessment of wetlands – from hydrological impact to ecological effects. In *Hydrology: Science and Practice for the 21st Century, Proceedings of the British Hydrological Society International Conference July 2004* (Volume II, eds B. WEBB, M. ACREMAN, C. MAKSIMOVIC, H. SMITHERS and C. KIRBY), pp. 198–212. British Hydrological Society, London.
- WHITFIELD, A. K., ELLIOTT, M., BASSET, A., BLABER, S. J. M. & WEST, R. J. (2012). Paradigms in estuarine ecology – a review of the Remane diagram with a suggested revised model for estuaries. *Estuarine and Coastal Shelf Science* **97**, 78–90.
- WIEDER, R. K., SCOTT, K. D., KAMMINGA, K., VILE, M. A., VITT, D. H., BONE, T., XU, B., BENSCOTER, B. W. & BHATTI, J. S. (2009). Postfire carbon balance in boreal bogs of Alberta, Canada. *Global Change Biology* **15**, 63–81.
- WILLOT, E. (2004). Restoring nature, without mosquitos? *Restoration Ecology* **12**, 147–153.
- WORRALL, F., EVANS, M. G., BONN, A., REED, M. S., CHAPMAN, D. & HOLDEN, J. (2009). Can carbon offsetting pay for upland ecological restoration? *Science of the Total Environment* **408**, 26–36.
- ZAK, D., WAGNER, C., PAYER, B., AUGUSTIN, J. & GELBRECHT, J. (2010). Phosphorus mobilization in rewetted fens: the effect of altered peat properties and implications for their restoration. *Ecological Applications* **20**, 1336–1349.
- ZEDLER, J. B. (2000). Progress in wetland restoration ecology. *Trends in Ecology & Evolution* **15**, 402–407.
- ZEDLER, J. B. (2003). Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Frontiers in Ecology and the Environment* **1**, 65–72.
- ZEDLER, J. B. (2004). Compensating for wetland losses in the United States. *Ibis* **146**, 92–100.
- ZEDLER, J. B. & KERCHER, S. (2005). Wetland resources: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* **30**, 39–74.

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