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Hydrological landscape settings of base-rich fen mires and fen meadows: an overview

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Abstract

Question: Why do similar fen meadow communities occur in different landscapes? How does the hydrological system sustain base-rich fen mires and fen meadows?

Location: Interdunal wetlands and heathland pools in The Netherlands, percolation mires in Germany, Poland, and Siberia, and calcareous spring fens in the High Tatra, Slovakia.

Methods: This review presents an overview of the hydrological conditions of fen mires and fen meadows that are highly valued in nature conservation due to their high biodiversity and the occurrence of many Red List species. Fen types covered in this review include: (1) small hydrological systems in young calcareous dune areas, and (2) small hydrological systems in decalcified old cover sand areas in The Netherlands; (3) large hydrological systems in river valleys in Central-Europe and western-Siberia, and (4) large hydrological systems of small calcareous spring fens with active precipitation of travertine in mountain areas of Slovakia.

Results: Different landscape types can sustain similar nutrient poor and base-rich habitats required by endangered fen meadow species. The hydrological systems of these landscapes are very different in size, but their groundwater flow pattern is remarkably similar. Paleo-ecological research showed that travertine forming fen vegetation types persisted in German lowland percolation mires from 6000 to 3000 BP. Similar vegetation types can still be found in small mountain mires in the Slovak Republic. Small pools in such mires form a cascade of surface water bodies that stimulate travertine formation in various ways. Travertine deposition prevents acidification of the mire and sustains populations of basiphilous species that elsewhere in Europe are highly endangered.

Conclusion: Very different hydrological landscape settings can maintain a regular flow of groundwater through the top soil generating similar base-rich site conditions. This is why some fen species occur in very different landscape types, ranging from mineral interdunal wetlands to mountain mires.

Keywords: Calcareous mire; Dune slack; Ecohydrology; Geohydrology; Paleo-ecology; Stability, Travertine formation.

Fen mires and fen meadows

A fen is a peatland fed hydrologically both by precipitation and groundwater, i.e. water that has been in contact with mineral soil or bedrock (Joosten & Clarke 2002). In the temperate zones of Europe, North America, and Asia, fens were originally the dominant mire type, but in most areas they have been drained for agriculture (Joosten & Clarke 2002). Such drained fens are generally still fed by groundwater or surface water but they have stopped accumulating peat. Although fen mires and drained fen (sedge) meadows (wet grasslands) are different ecosystems, they have many plant species in common (Grootjans & van Diggelen 1995).

Fen mires and fen meadows are highly valued in nature conservation due to their high species biodiversity and the occurrence of many highly endangered (‘Red List’) species (Bedford & Godwin 2003). Both in Europe and in North America this biodiversity is threatened by hydrologic changes related to high intensity agriculture and urban development (Middleton & Grootjans In press).

Aim and outline of the review

The aim of this review is to elucidate the landscape ecological settings of fen mire communities belonging to the alliance *Caricion davalliana* (small-sedge communities of base-rich or calcareous habitats) and of fen meadows of the alliance *Molinion* (unfertilized mown grasslands), which have often originated from moderately drained base-rich fens. These two ecosystem types are often found together in a wide variety of landscape types ranging from small interdunal wetlands on mineral soil to large river valleys with actively accumulating peat. We will compare several hydrological systems that sustain habitat conditions of these base-rich fen mires and fen meadows, and will show that a proper knowledge of the hydrological systems is a precondition for the long-term conservation management of endangered fen species.

Whereas in the past natural fens remained treeless and diverse without management (Succow & Joosten 2001), nowadays most fens and fen meadows in Europe and North America require regular mowing, grazing or burning (van Andel & Arondsen 2006) to control the increased growth of tall grasses, sedges, shrubs or trees caused by drainage or eutrophication (Middleton et al. 2006).

After a short overview of the history of ecohydrological research in fen and fen meadows in the last century, we will discuss the different hydrological systems, which create and sustain habitats of basiphilous plant species including (1) small hydrological systems of coastal interdunal wetlands (dune slacks) and (2) small hydrological systems in a very acid cover sand landscape (heath pools) in The Netherlands; (3) large hydrological systems of Central-European and West-Siberian river valleys, and (4) hydrological systems of small calcareous spring fens in mountain areas of Slovakia. Endangered plant species that may occur in all these landscape types include *Schoenus nigricans, Eleocharis quinqueflora, Juncus alpino-articulatus, Carex pulicaris, Parnassia palustris, Epipactis palustris, Dactylorhiza incarnata, Herminium monorchis* and *Liparis loeselii*.

The groundwater flow pattern of these systems promotes base-rich conditions or even travertine (tufa) formation (i.e. the deposition of $CaCO_3$, cf. Almendinger & Leete 1998a,b) in the top soil, which prevents soil acidification and reduces nutrient availability (Boyer & Wheeler 1989; Lamers et al. 1998). Travertine deposition is often linked to the occurrence of large numbers of basiphilous fen mire and fen meadow species.

Recent paleo-ecological research in East German and Western Siberian river valleys provides a detailed insight into the development of these fens over the last 9000 years. We will compare the reconstructed hydrology and the conditions for travertine deposition in these fens with those of recent groundwater fed spring mires in the Slovak Republic, that harbour large populations of endangered fen meadow species. These systems are still depositing travertine and provide an interesting opportunity to unravel hydrological conditions that promote travertine deposition.

Finally we will discuss the vulnerability of hydrological systems to hydrological and climatic changes in the landscape.

Classic views on mires

Historically, peatlands were distinguished on the basis of their situation, and their usage, both as intact wetlands and after peat extraction, leading to the identification of two main mire types:

- **Bogs** raised above the surrounding landscape. Because of their low productivity, bogs were rarely used for agriculture. After peat extraction, which was normally carried out under dry conditions following drainage, a mineral subsoil suitable for agriculture remained.
- **Fens** situated in depressions. Because of their somewhat higher nutrient availability, fens were of interest for agriculture, especially for collecting hay and litter. After peat extraction, which was carried out by dredging, open water remained.

Most mire and peatland typologies have been based on hydrologic conditions, reflecting the central role of water in peat formation and peatland use.

Du Rietz (1949) published a classic article on the differentiation of bogs and fens on the basis of the chemical composition of the mire water. Du Rietz (1954) identified the '*Mineralbodenwasserzeigergrenze*', the limit of mineral soil water influence in a mire, indicated by the occurrence of plant species that prefer a somewhat higher pH than most bog species. He was certainly not the first to classify mires on the origin and chemical properties of the water supply. Dau (1823) had recognized that bogs, in contrast to fens, are fed 'from merely rain and dew of heaven' and are 'not fed by earth'. Weber (1902) had furthermore discovered that vegetation type is not only dependent on the nature of water chemistry, but also on the amount of flow of water. Subsequently Kulczyński (1949) stressed the importance of water flow by introducing the concepts *rheophilous* ('stream loving') and *ombrophilous* ('rain loving') mires. Sjörs (1950), Malmer (1962) and Moore & Bellamy (1974) distinguished a whole range of 'hydrological mire types' on the basis of water composition, which lead to the widespread concepts of 'poor fen', 'intermediate fen', and 'rich fen'. Succow (1988) proposed a bivariate system of 'ecological mire types' by separating nutrient availability (trophic conditions) from base saturation (acidity). He also identified characteristic plant species and vegetation types for his mire types.

These typologies based on vegetation differences depending on water quality were paralleled by approaches focusing on the genesis of peatlands. A first distinction was made around 1900 between 'terrestrialization', the development of peat in open water, and 'paludification', the accumulation of peat directly over a paludifying mineral soil (Gams & Ruoff 1929). Kulczyński (1949) also pointed at the importance of water movement for mire development (Moore & Bellamy 1974; Ivanov 1981). Succow (1988) elaborated these ideas into a system of ‘hydrologic - genetic mire types’ (or shortly ‘hydrogenetic’, i.e. based on the hydrology and genesis of the peatland) which were formalized by Succow & Joosten (2001) and Joosten & Clarke (2002) on the basis of feedback mechanisms between peat formation, water flow and water level fluctuations. Hydrogenetic mire classification, which focuses on the hydrological processes facilitating peat formation in the landscape, was until recently largely descriptive.

Quantitative mire hydrology was studied and reviewed by Baden & Eggelsman (1963), Ivanov (1981), Ingram (1983), and Heathwaite (1995), but most of these studies concentrated on rainwater fed bogs. Hydrological systems analysis, combining hydrology and hydrogeochemistry, was initiated by hydrologists (Tóth 1962; Engelen & Jones 1986) and applied to fens (Schot & Molenaar 1992; Komor 1994; Grootjans & van Diggelen 1995; Wassen et al. 1990, 1996; Wassen & Joosten 1996; Wheeler 1999; Loos & Schipper 2003) and also bogs (Siegel & Glaser 1987; Glaser 1992; Glaser et al. 1997). The necessity of a hydrological system approach was elegantly demonstrated by Stuyfzand (1993) who showed that the interpretation of solely hydraulic head differences in shallow dune lakes is insufficient for reconstructing groundwater flow (Fig. 1). Especially in dune areas with coarse sand, vertical head gradients are too small to be measured adequately with manual water level measurements, which are accurate to about 0.5 cm. Temperature differences and the chemical composition of ground- and surface water provide a much better insight into groundwater flow paths. Similarly van Wirdum (1991, 1993) measured temperature and Electrical Conductivity (EC) gradients in peat profiles to detect changes in surface water flow related to the development of rainwater lenses in floating fens in The Netherlands.

Much research has been done in The Netherlands on the hydrological setting of *Cirsio-Molinietum* ‘litter meadow’, a nutrient-poor, groundwater fed fen meadow type, of which the small remnants are endangered due to drainage of surrounding agricultural fields (Wassen et al. 1996; van Diggelen 1998; de Mars et al. 1996; van Duren et al.1998; Jansen et al. 2000). Schot & Molenaar (1992) combined modelling of fen hydrology with the analysis of groundwater quality and natural isotopes (see also Grootjans et al. 1996).

Different hydrological systems can sustain similar fen mire / fen meadow types

An interesting finding from these studies is that hydrological conditions can create habitats with similar vegetation types in a wide range of landscape types. Small-sedge communities (*Caricion davallianae*) with many Red List species occur in coastal dune slacks on sandy soils (Lammerts & Grootjans 1998), in lowland brook valleys on peat soils (Succow & Joosten 2001), but also in alpine calcareous spring mires (Ellenberg 1978). *Cirsio-Molinietum* fen meadows are found in small first-order stream catchments that dry out at the end of summer (Fig. 2), but also in landscapes influenced by larger regional groundwater systems (Jansen et al. 2000). Some *Cirsio-Molinietum* communities even

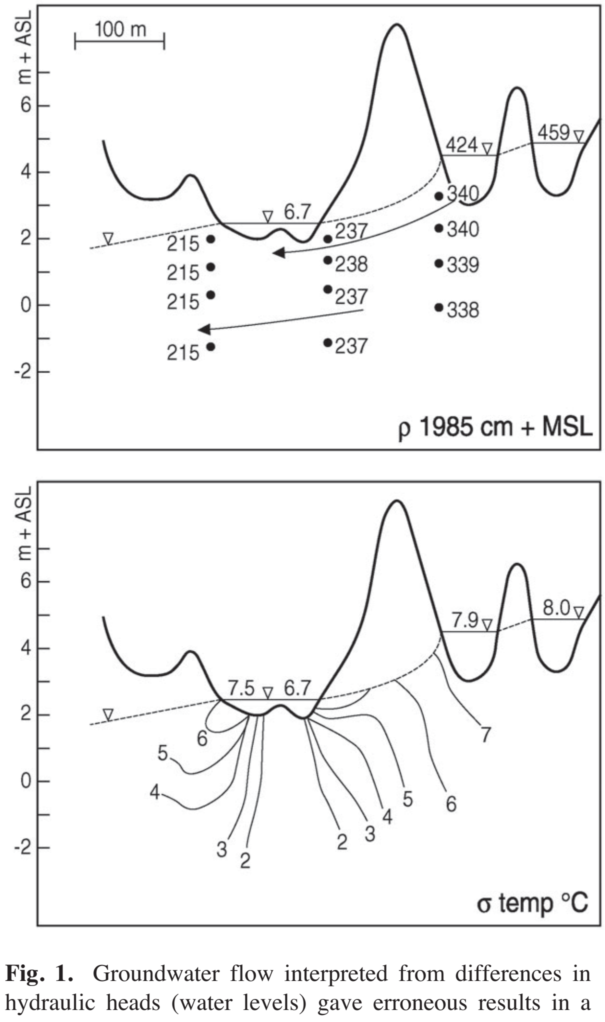

Fig. 1. Groundwater flow interpreted from differences in hydraulic heads (water levels) gave erroneous results in a coastal dune slack (**a**). Measurements of temperature differences in the profile (**b**) showed that the groundwater entered the slack at the right side, flowed through the slack as surface water and proceeded as infiltration water at the left side (after Stuyfzand 1993).

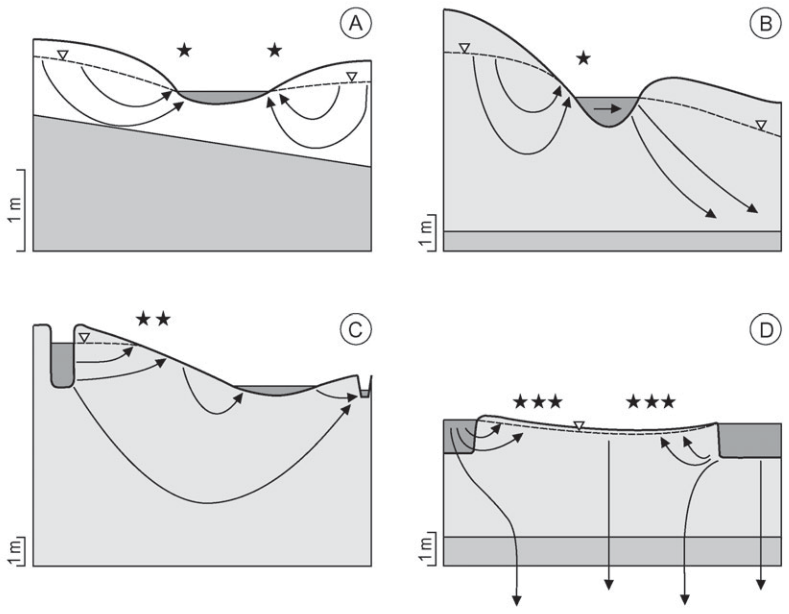

Fig. 2. The fen meadow community *Cirsio-Molinietum* (indicated by *) occurs in The Netherlands under various hydrological conditions. **A** = heathland pool situated above shallow loam layer with groundwater supply from local sand ridges; **B** = local (small) hydrological system with through flow of groundwater; **C** = artificial hydrological system with lateral discharge of calcareous surface water from large canals; **D** = surface water system with discharge of calcareous surface water from ditches (modified after Jansen et al. 2000).

have an entirely anthropogenic origin and depend on seepage from canals (cf. Boeye et al. 1996).

Groundwater-fed fens are essentially ‘through-flow’ systems, in which geochemical processes along the flow path reduce plant nutrient availability in the rooting zone. The geochemical interactions at the interface of discharging groundwater and flowing surface water were discussed by Stuyfzand (1993) for small dune ponds that are used to purify surface water from the large Dutch rivers to produce drinking water for the large Dutch cities. Polluted surface water from recharge ponds infiltrates into the dunes to exfiltrate at one side of a lower lying ‘through-flow lake’ where it proceeds as surface water, to finally infiltrate at the other side of the lake. A similar hydrological system was described for natural dune slacks with nutrient-poor pioneer stages of the *Caricion davallianae*, which are rich in fen species (Grootjans et al. 1996; Adema et al. 2002; Fig. 3). The most nutrient-poor species occur between the seepage and the infiltration zone where active travertine formation takes place (Sival et al. 1998).

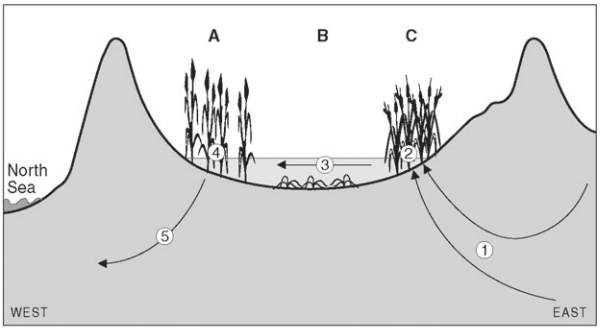

Fig. 3. Schematic presentation of the hydrological functioning of a small dune slack on the Wadden island of Texel, The Netherlands; **A** = eutrophic reed (*Phragmites australis*); **B** = oligotrophic pioneer vegetation dominated by *Littorella uniflora*; **C** = eutrophic sedge vegetation (*Carex riparia*). 1 = incoming calcium and iron-rich groundwater; 2 = exfiltration of groundwater; 3 = surface water flow with precipitation of iron and calcium; 4 = infiltration of surface water; 5 = outgoing calcium and iron-poor infiltration water (after Adema et al. 2002).

Jansen et al. (2001) illustrated how local and regional groundwater systems may interact to sustain fen meadow species of base-rich habitats in small pools within acid heathlands on deeply leached sandy soils. The vegetation survives in these fens because of a regional hydrological system that discharges deep groundwater in the heath pools only during early spring when raised water levels in tiny hills cause a water flow towards the pools. At the end of spring, all groundwater discharge stops and the following autumn rains fill the pools with rainwater. If the discharge of calcareous groundwater in spring would stop, e.g. by groundwater abstraction from the deep aquifer, the pool system would rapidly acidify and would lose most of its biodiversity.

Loos & Schipper (2003) studied a very large (50 km^2) pristine fen mire system on a lower river terrace along the River Ob in West-Siberia. They analysed the chemical composition of the water flowing in the fen vegetation and in the peat layers below. With a 2D vertical groundwater model (MODFLOW) groundwater flow paths were reconstructed using MODPATH (Loos & Schipper 2003; Fig. 4). Water levels were very close to the surface throughout the growing season, demon-

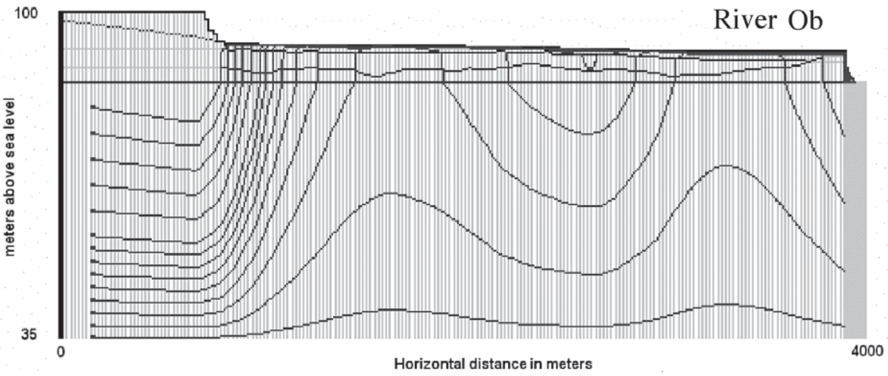

Fig. 4. Hydrological modeling of groundwater flow in the River Ob,western Siberia (after Schipper & Loos 2003). The water flow is from left to right.

strating the importance of groundwater discharge. The modelled groundwater flux to the fen varied over the 3 km wide fen from 0.02 $m.d^{-1}$ close to the upland to 0.002 $m.d^{-1}$ halfway to the Ob River. The discharging groundwater has infiltrated in a 30 - 50 km wide upland zone parallel to the fen. Most of the water flowing over and through the fen vegetation consisted of discharging groundwater because the mean groundwater flux over the whole profile (0.002 $m.d^{-1}$) is ca. 2.5 - 4 times larger than the supply of net precipitation to the mire. Most of the nutrients were transported through a water layer between the peat and the floating roots of the fen vegetation. Also, the nutrient balance showed that the groundwater discharge was several orders of magnitude more important than precipitation. Vegetation change can be expected when groundwater levels in the peat are lowered and the permeability of the peat decreases (Wassen et al. 2002; Schot et al. 2004).

Peat-forming fens

All groundwater fed fens receive water from the associated recharge area and hence reflect features of the regional hydrology. Large through-flow fens, moreover, raise their water level and that of their surroundings autogenously, leading to the expansion of fens and the origin of spring mires on progressively higher positions in the landscape. An example of such a switch in peat formation was presented by Michaelis (2002) who studied the Holocene development of the extensive North German Recknitz valley fen (see also Clausnitzer 1996). A transect across the valley shows a distinct zone of 'brown moss' peat, consisting of fen moss species at a site where groundwater entered the mire. Travertine (tufa) deposits are also present (Fig. 5).

In a late stage of peat development, the inflow of groundwater can become locally insufficient to sustain a groundwater-fed fen vegetation and a bog can start to develop in the centre of the fen. Shifts from bog to fen can also occur. Michaelis (2002) found a small mineral island within a mire that was overgrown with peat and changed from groundwater recharge to groundwater discharge conditions between 9300 and 6000 BP. The vegetation changed from *Pinus* forest into small sedge vegetation with some *Phragmites australis* and much *Homalothecium nitens*. *Epipactis palustris* was present for a long time, indicating basiphilous conditions. Some 200 m further down slope, travertine was deposited in sedge vegetation with *Drepanocladus* species. Around 5000 BP, this process stopped because of a rise in water level and subsequent inundation as a result of marine

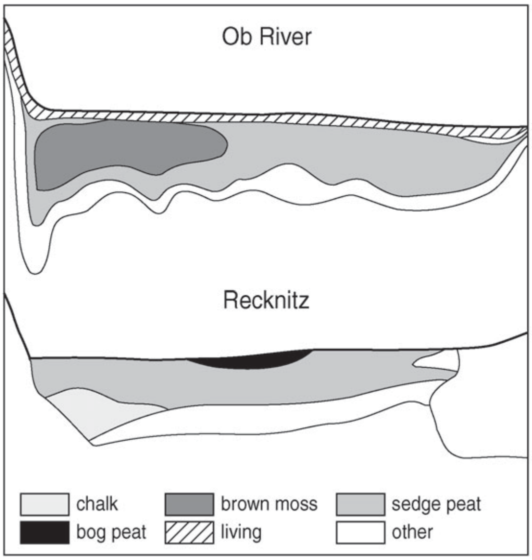

Fig. 5. Peatland stratigraphy in a transect across a mire along the River Ob in western Siberia (after Schipper et al. 2006) and in a transect across the Recknitz valley in Germany (after Clausnitzer 1996).

transgression (the '*Littorina* transgression'). Schult (2002) found a similar travertine deposition in the Trebel valley, but over a longer period (until ca. 3000 BP), indicating that hydrological conditions rather than climate were responsible for travertine deposition.

These paleo-ecological studies in North German valley mires show that shifts in hydrological conditions may lead to shift from bog to fens and *vice versa*. The vertically homogenous peats, however, show that peat-forming conditions in such fens generally remained constant over thousands of years in spite of climatic and hydrologic changes (cf. Couwenberg et al. 2001). This stability was probably caused by the large thickness of the peat, enabling considerable oscillation and preventing both flooding and desiccation of the mire surface (Joosten & Clarke 2002).

Present travertine formation in mires

Travertine formation in valley mires was once a widespread phenomenon in North-Germany and Poland (Succow & Joosten 2001; Wolejko 1994), but nowadays actual deposition of travertine is a rare phenomenon in the temperate zones of Europe. It has been reported from lowland valley fens in Northeast Poland (Sidra river, tributary to the Biebrza), South Sweden, Estonia (Tyler 1981) and Germany (Kloss 1965; Pietsch 1984), and also from sub-montane spring fens in England (Boyer & Wheeler 1989), Switzerland, France, Austria (Steiner 1992), Czech Republic and Slovakia (Carpathian Mountains; Hájek et al. 2002). Travertine formation depends on lime dissolution in groundwater on its way to a fen. As an example we will discuss travertine formation in an almost pristine spring fen near the village of Strba close to the High Tatra Mountains (Slovakia), where travertine is still being formed in pools with *Drepanocladus* species, *Menyanthes trifoliata*, and *Chara* species (Fig. 6). The moss species *Homalothecium nitens* is present in large numbers at slightly elevated, less calcareous sites. Travertine formation is a recent phenomenon here and mainly occurs in the top soil layer where supersaturated groundwater is discharging in a series of small pools (Grootjans et al. 2005). During summer the surface water of these pools is warmed up. At higher temperatures, less CO_2 can be dissolved than at low temperatures and outgassing of CO_2 leads to the precipitation of $CaCO_3$. Algae, moss species, and some water plants, such as *Chara* species, accelerate this travertine formation by using CO_2 in the pools as a carbon source, often leaving the imprints of, for instance, mosses in the travertine (Michaelis 2002). Precipitation of $CaCO_3$ prevents acidification and associated eutrophication of the topsoil and sustains the very high biodiversity of such fens.

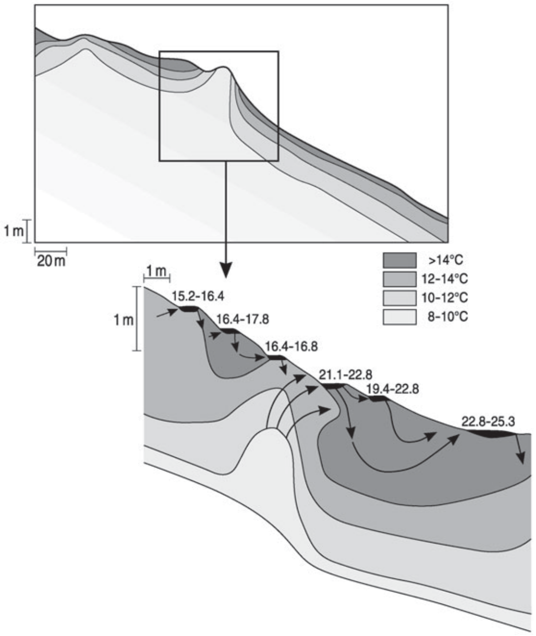

Fig. 6. Temperature profiles in the spring mire Štrba in Slovakia showing the interpreted groundwater flow through a cascade of pools (black). Above the pools the temperatures of the incoming water groundwater and the out flowing surface water have been indicated. Note that the groundwater is warmed up as a consequence of warming of surface water in the pools.

Stability of fens and fen meadows

Paleo-ecological research (Table 1) has shown that basiphilous fen vegetation in river valleys can be stable for several thousands of years (Michaelis 2002) and that fen meadows of the *Caricion davallianae* and the *Cirsio-Molinietum* are stable for several hundreds of years, although their origin is relatively recent (from the early Middle Ages onwards; Janssen 1972; Rybníčková et al. 2005).

Small groundwater-fed systems are very vulnerable to hydrological changes and climate change. Due to the lowering of groundwater tables in the vicinity, the regeneration prospects of most dune slacks and heath pools with basiphilous vegetation, for instance, are very small (Grootjans et al. 2002; Jansen et al. 1996; Jansen et al. 2000; van den Hoek 2005). Even when the local site conditions are temporarily improved by removal of accumulated litter and the eutrophicated or acidified topsoil, the changed hydrology limits the life span of 'restored' target communities to 10 years or less (Adema et al. 2001; Grootjans et al. 2002). Van Duren et al. (1998) presented a clear case that restoration of a lake side fen meadow in the Dutch lowlands has become

Table 1. Stability of two plant communities after formation, disturbance or restoration.

Plant community Habitat type	Years stable	Reference
Caricion davallianae		
Dune slack	5-10	Grootjans et al. (2002)
Fen meadow	> 15	Klötzli (1987)
Dune slack	> 40	Grootjans et al. (2002)
Dune slack	80	Adema et al. (2002)
Dune slack	> 85	Grootjans et al. (2002)
Spring mire	250-500	Rybníčková et al. (2005)
Percolation mire	2000-3000	Michaelis (2002)
Cirsio-Molinietum		
Fen meadow	< 1	Jansen et al. (1996)
Fen meadow	< 2	van Duren et al. (1998)
Fen meadow	5-10	van den Hoek (2005)
Fen meadow	> 10	Pfadenhauer & Heinz (2004)
Fen meadow	> 11	Grootjans et al. (2002)
Fen meadow	> 15	Jansen et al. (2004)
Fen meadow	500 - 800	Janssen (1972)

impossible due to irreversible changes in the local hydrological system. Attempts to restore the fen meadow by removing the acidified top soil and purify the inundation water did not lead to the return of target species, not even after the reintroduction of the species. Due to severe lowering of the groundwater level in deeply drained agricultural polder areas (due to peat subsidence of several meters per century; cf. Hutchinson 1980), the fen meadow site has changed from a groundwater discharge into a groundwater recharge area and acidification continued.

Sloping fens can easily shift from peat accumulating into eroding systems (Wołejko et al. 1994). Digging of drainage ditches or lowering of lake levels may start uncontrolled erosion that often ends in the total destruction of the mire. Due to rapid peat mineralization such peatlands become very eutrophic leading to the invasion of tall herbs, such as *Urtica dioica*, shrubs, and trees.

Extensive fen systems sustained by large hydrological systems are less vulnerable to local drainage, but in NW Europe, large scale interference with the regional hydrology eventually has split up the large fen systems into many small fens, each with a small local hydrological system (Wassen et al. 1990). Comparative ecohydrological research in The Netherlands, eastern Germany and Poland showed that the large fen systems in these countries functioned similarly in the past, but that the Dutch sites now only constitute small remnants of fen meadow in polder areas with a totally anthropogenic hydrological system (Wassen et al. 1996; van Diggelen 1998). van Diggelen (1998) calculated that under the prevailing conditions of deep drainage, groundwater abstraction, and continuous infiltration, the buffering capacity of the top layer will be depleted and the fen meadow remnants will acidify within 40 years.

Biogeochemical constraints on nutrient availability

In natural fens, nitrogen is often the primary limiting nutrient, while regular harvesting eventually results in phosphorus or even potassium limitation (van Duren & Pegtel 2000; Olde Venterink et al. 2002). Experimental research has shown that Ca can limit P-availability in very calcareous fens (Boyer & Wheeler 1989) but in less calcareous fens, Fe and Al are more important for phosphate fixation (Boeye et al. 1996). At low redox potentials in water saturated fen peat, nitrogen availability is also strongly reduced by denitrification, particularly in the areas with a high groundwater discharge (Brady & Weil 1999). If groundwater discharge decreases, higher nitrogen concentrations in the rooting zone of the vegetation can be expected, in particular when the atmospheric deposition is high. In The Netherlands, atmospheric N-deposition is higher (25 - 40 $kg.ha^{-1}.a^{-1}$) than the critical N-load for fens (Bobbink et al. 1998). Consequently, vegetation succession is accelerated and fast growing species start to dominate at the cost of slow growing fen species despite regular mowing. A regular discharge of anaerobic groundwater in areas with a low atmospheric N-deposition, therefore, stabilizes nutrient cycling at a low level. Moreover, sulphate concentrations in groundwater-fed fens and fen meadows are generally very low. If the groundwater discharge diminishes, the sulphate concentration may increase due to the increased influx of sulphate-rich surface water. An increase in the sulphate concentration can increase nutrient cycling in the peat soils due to microbial sulphate reduction (Lamers et al. 2002). Sulphate reduction oxidizes organic material and produces sulphide, which in most fens and fen meadows is chemically bound by iron (FeS and FeS_2; pyrite). When sulphide production is very high and iron is in short supply, the produced sulphide can interfere with phosphate binding to iron hydroxides, and phosphate concentrations may increase in the soil pore water, thus stimulating the growth of the vegetation (Lucassen et al. 2004). In phosphorus-limited systems, such as most base-rich fens and fen meadows (Wassen et al. 2005), such internal eutrophication can lift P-limitation and make the fen or fen meadow very susceptible to increased atmospheric nitrogen deposition (Lamers et al. 1998). In summary, anoxic iron-rich groundwater stabilizes nutrient cycling at a low level, whereas oxic surface water stimulates nutrient cycling, speeds up the succession to more productive stages, thus destabilizing the typical fen mire and fen meadow ecosystem. This does not mean that permanently high groundwater levels in fen mires and fen meadows will always keep nutrient availability at a low level. On the contrary, permanently high water levels may also lead to a reduction of Fe^{3+} to Fe^{2+}, which leads to a less firm binding of phosphate to iron. Periodic local desiccation of the upper peat layer during summer, which is a natural phenomenon in fens, is important because it enables the soil to retain phosphates through Fe^{3+}-fixation. If FeS_x is present in the top soil, its oxidation increases the reactive Fe^{3+} concentration, stimulating P-binding in the top layer (Lucassen et al. 2005). This pyrite oxidation may cause large acidification problems in drained fens, due to its high acid production, but in well developed fens, slow flowing groundwater stimulates the precipitation of iron and $CaCO_3$ in the root zone, thus stabilizing nutrient cycling and preventing acidification at the same time.

Future of fen and fen meadows

Paleo-ecological studies of fen remnants have been instrumental in showing that some fen systems once were very stable without human management. In former times, hydrological systems provided natural fens with a large supply of base-rich and iron-rich groundwater that sustained nutrient-poor and species-rich fen vegetation for several centuries, without management by man (Couwenberg et al 2001; Glaser et al. 2004). A slow groundwater flow in fen systems seems to be essential for maintaining a high biodiversity as it prevents peat erosion and stimulates the co-precipitation of phosphate with iron and $CaCO_3$ in the root zone, maintaining nutrient cycling at a low level.

Very different hydrological landscape settings can maintain such a regular flow of groundwater through the top soil generating similar habitat conditions for many fen species. This is why some species occur in very different landscape types, ranging from mineral interdunal wetlands to mountain mires.

Restoration measures aimed at restoring fen mires and fen meadows should, therefore, aim at restoring the through-flow of anaerobic groundwater. In order to take adequate measures, it is essential to study the hydrological systems that stabilize the site conditions of fen mires and fen meadows. Long-term experience (> 10 years) has clearly shown that restoration prospects of severely degraded sites are very poor. The most successful restoration has been achieved in the least affected sites. Therefore, the future of fen mires and fen meadows is in the conservation of unaffected sites.

References

Adema, E.B., Grootjans, A.P., Petersen, J. & Grijpstra, J. 2002. Alternative stable states in a wet calcareous dune slack in The Netherlands. *J. Veg. Sci.* 13: 107-114.

Almendinger, J.E. & Leete, J.H. 1998a. Peat characteristics and groundwater geochemistry of calcareous fens in the Minnesota River basin, USA. *Biogeochemistry* 43: 17-41.

Almendinger, J.E. & Leete, J.H. 1998b. Regional and local hydrogeology of calcareous fens in the Minnesota River basin, USA. *Wetlands* 18: 184-202.

Baden, W. & Eggelsman, R. 1963. Zur Durchlässigheit der Moorböden. *Z. Kulturtechn.* 4: 226-254.

Bedford, B.L. & Godwin, K.S. 2003. Fens of the United States: distribution, characteristics, and scientific connection versus legal isolation. *Wetlands* 23: 608-629.

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. *J. Ecol.* 86: 717-738.

Boeye, D., Van Haesebroeck, V., Verhagen, B., Delbaere, B., Hens, M. & Verheyen, R.F. 1996. A local rich fen fed by calcareous seepage from an artificial river water infiltration system. *Vegetatio* 126: 51-58.

Boyer, M.L.H. & Wheeler, B.D. 1989. Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. *J. Ecol.* 77: 597-609.

Brady, N.C. & Weil, R.R. 1999. *The nature and properties of soils*. 12th ed. Prentice-Hall, London, UK.

Clausnitzer, U. 1996. *Vegetationskundlich-landschaftsökologische Untersuchungen im Flusstalmoor der Recknitz zwischen Güstrow und Ribnitz-Damgarten als Grundlage für Maßnahmen zur Renaturierung und naturgemässen Bewirtschaftung*. Unpubl. Report, cited in Michaelis (2002).

Couwenberg, J., De Klerk, P., Endtmann, E. Joosten, H. & Michaelis, D. 2001. In: Succow, M. & Joosten, H. (eds.) *Landschafsökologische Moorkunde* (2nd ed.), pp. 399-403. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, DE.

Dau, J.H.C., 1829. *Die Torfmoore Seelands*. Gyldendahl und Hinrichs, Kopenhagen, DK, Leipzig, DE.

Dau, J.H.C. 1823. *Neues Handbuch über den Torf, dessen Natur, Entstehung und Wiedererzeugung*. J.E. Hinrischssche Buchhandlung, Leipzig, DE.

De Mars, H., Wassen, M.J. & Peeters, W.H.M. 1996. The effect of drainage and management on peat chemistry and nutrient deficiency in the former Jegrzenia floodplain (NE Poland). *Vegetatio*: 126: 59-72.

Du Rietz, G.E. 1949. Huvudenheter och huvudgränser i svensk myrvegetation. *Sven. Bot. Tidskr.* 43: 274-309.

Du Rietz, G.E. 1954. Die Mineralbodenwasserzeigergrenze als Grundlage einer natürlichen Zweigliederung der nord- und mitteleuropäischen Moore. *Vegetatio* 5/6: 571-585.

Ellenberg, H. 1978. *Vegetation Mitteleuropas mit den Alpen*. Verlag Ulmer, Stuttgart, DE.

Engelen, G.B. & Jones, G.P. 1986. *Developments in the analysis of groundwater flow systems*. International Association of Hydrological Sciences, Wallingford, UK.

Gams, H. & Ruoff, S. 1929, Geschichte, Aufbau und Pflanzendecke des Zehlaubruches. *Schr. Phys.-Ökon. Ges. Königsberg*

66: 1-192.

Glaser, P.H. 1992. Raised bogs in eastern North America: regional controls on species richness anf floristic assemblages. *J. Ecol*. 80: 535-554.

Glaser, P.H., Siegel, D.I., Romanowicz, E.A. & Shen, Y.P. 1997. Regional linkages between raised bogs and the climate, groundwater, and landscape features of northwestern Minnesota. *J. Ecol*. 85: 3-16.

Glaser, P.H., Siegel, D.I, Reeve, A.S., Janssens, J.A. & Janecky, D.R. 2004. Tectonic drivers for vegetation patterning and landscape evolution in the Albany River region of the Hudson Bay Lowlands. *J. Ecol*. 92: 1054-1070.

Grootjans, A.P. & van Diggelen, R. 1995. Assessing the restoration prospects of degraded fens. In: Wheeler, B.D., Shaw, S.C., Foyt, W.J. & Robertson, R.A. (eds.) *Restoration of temperate wetlands*, pp. 73-90. John Wiley & Sons, Chichester, UK.

Grootjans, A.P., Sival, F.P. & Stuyfzand, P.J. 1996. Hydrogeochemical analysis of a degraded dune slack. *Vegetatio* 126: 27-38.

Grootjans, A.P., Geelen, L., Jansen, A.J.M. & Lammerts, E.J. 2002. Restoration of coastal dune slacks. *Hydrobiologia* 478: 181-203.

Grootjans, A.P., Alserda, A., Bekker, R.E.M., Janáková, M., Kemmers, R.F., Madaras, M., Stanova,V., Ripka, J., van Delft, B. & Wołejko, L. 2005. Calcareous spring mires in Slovakia; Jewels in the Crown of the Mire Kingdom. In: Steiner, G.M. (ed.) Mires, from Siberia to Tierra del Fuego. *Stapfia* 85: 97-115.

Hájek, M., Hekera, P. & Hajkova, P. 2002. Spring fen vegetation and water chemistry in the western Carpathian Flysch zone. *Folia Geobot*. 37: 205-224.

Heathwaite, A.L. 1995. Overview of the hydrology of British wetlands. In: Hughes, J. & Heathwaite, L. (eds.). *Hydrology and hydrochemistry of British wetlands,* pp. 11-20. Wiley and Sons, Chichester, UK.

Hutchinson, J.N. 1980, The record of peat wastage in the East Anglian fenland of Holme Post, 1848 - 1978 A.D. *J. Ecol*. 68: 229-249.

Ingram, H.A.P. 1983. Hydrology. In: Gore, A.J.P. (ed.) *Mires: swamp, bog, fen, and moor*. *Ecosystems of the World Vol. 4A, General studies,* pp. 67-158. Elsevier, Amsterdam, NL.

Ivanov, K.E. 1981. *Water movement in mirelands*. [Translated by Thomson, A. & Ingram, H.A.P. from Ivanow, K.E. 1975, Vodoobmen v bolotnykn landshafter.] Academic Press, London, UK.

Jansen, A.J.M., de Graaf, M.C.C. & Roelofs, J.G.M. 1996. The restoration of species-rich heathland communities in the Netherlands. *Vegetatio* 126: 73-88.

Jansen, A.J.M., Grootjans, A.P. & Jalink, M. 2000. Hydrology of Dutch *Cirsio-Molinietum* meadows: prospects for restoration. *Appl. Veg. Sci*. 3: 51-64.

Jansen, A.J.M., Eysink, A.Th.W. & Maas, C. 2001. Hydrological processes in a *Cirsio-Molinietum* wet meadow: implications for restoration. *Ecol. Engin*. 17: 3-20.

Janssen, C.R. 1972. The palaeoecology of plant communities in the Dommel valley, North Brabant, The Netherlands. *J. Ecol*. 60: 411-437.

Joosten, H. & Clarke, D. 2002. *Wise use of peatlands*. International Mire Conservation Group, International Peat Society, Jyväskylä, FI.

Kloss, K. 1965. Schoenetum, Juncetum subnodulosi und *Betula pubescens*-Gesellschaften der kalkreichen Moorniederungen Nordost-Mecklenburgs. *Feddes Rep. Beih*. 142: 65-117.

Klötzli, F. 1987. Disturbance in transplanted grasslands and wetlands. In: van Andel, J., Bakker, J.P. & Snaydon, R.W. (eds.) *Disturbance in grasslands*, pp. 79-96. Geobotany 10, Junk Publishers, Dordrecht, NL.

Komor, S.C. 1994. Geochemistry and hydrology of a calcareous fen within the Savage Fen wetland complex, Minnesota, USA. *Geochem. Cosmochem. Acta* 58: 3353-3367.

Kułczyński, S. 1949. Torfowiska Polesia. Peat bogs of Polesie. *Mem. Acad. Pol. Sci. Lett. Sci. Mat. Nat. Ser. B: Sci. Nat.* 15: 1-359.

Lamers, L.P.M., Tomassen, H.B.M. & Roelofs, J.G.M. 1998. Sulphate-induced eutrophication and phytotoxicity in freshwater wetlands. *Environ. Sci. Techn*. 32: 199-205.

Lamers, L.P.M., Smolders, A.J.P. & Roelofs, J.G.M. 2002. The restoration of fens in the Netherlands. *Hydrobiologia* 478:107-130.

Lammerts, E.J. & Grootjans, A.P. 1998. Key environmental variables determining the occurrence and life span of basiphilous dune slack vegetation. *Acta Bot. Neerl*. 47: 369-392.

Loos, S. & Schipper, A. 2003. Hydrological and hydrochemical system analysis of Ob valley mire (Western Siberia). *Landschap* 20: 33-37. (In Dutch with English summary.)

Lucassen, E.C.H.E.T., Smolders, A.J.P., Van de Crommenacker, J. & Roelofs, J.G.M. 2004. Effects of stagnating sulphate-rich water on the mobility of phosphorus in freshwater wetlands. *Arch. Hydrobiol*. 160: 117-131.

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 Soil* 269: 109-115.

Malmer, N. 1962. Studies on mire vegetation in the archaean area of southwestern Götaland. I. Vegetation and habitat conditions on the Åkhult mire. *Opera Bot*. 7: 1-322.

Michaelis, D. 2002. *Die spät- und nacheiszeitliche Entwicklung der natürlichen Vegetation von Durchströmungsmooren in Mecklenburg-Vorpommern am Beispiel der Recknitz*. Dissertationes Botanici 365, Cramer Berlin, DE.

Middleton, B. & Grootjans, A.P. In press. Management and Restoration perspectives of fen/ sedge meadows. In: Verhoeven, J.T.A., Beltman, B.B. & Bobbink, R. (eds.) *Ecological studies 191*, Springer Verlag, Berlin, DE.

Middleton, B. & Grootjans, A.P., Jensen, K., Olde Venterink, H. & Margóci, K. In press. Fen management and research perspectives: an overview. In: Verhoeven, J.T.A., Beltman, B.B. & Bobbink, R. (eds.) *Ecological Studies 191*. Springer Verlag, Berlin, DE.

Middleton, B.A., Holsten, B. & van Diggelen, R. 2006. Biodiversity management of fens and fen meadows by grazing, cutting and burning. *Appl. Veg. Sci*. 9: 307-316.

Moore, P.D. & Bellamy, D.J. 1974. *Peatlands*. Elek Science, Londen, UK.

Olde Venterink, H., Pieterse, N.M., Belgers, J.D.M., Wassen, M.J., de Ruiter, P.C. 2002. N, P and K budgets along nutrient availability and productivity gradients in wetlands. *Ecol. Appl.* 12: 1010-1026.

Pfadenhauer, J. & Heinz, S. 2004. *Renaturierung von niedermoortypischen Lebensräumen; 10 Jahre Niedermoormanagement im Donaumoos*. Bundesamt für Naturschutz, Bonn-Bad Godesberg, DE.

Pietsch, W. 1984. Die Standortverhältnisse im Naturschutzgebiet 'Kalktuf-Niedermoor' (Vorderrhön). *Arch. Naturschutz u. Landschaftsforsch*. 24: 259-273.

Rybníčková, E., Hájkova, P. & Rybníček, K. 2005. The origin and development of spring fen vegetation and ecosystems-palaeogeobotanical results. In: Poulíčková, A., Hájek, M. & Rybníček, K. (eds.) *Ecology and palaeoecology of spring fens of the West Carpathians*. University of Olomouc/ Academy of Science of the Czech Republic/ University of Brno, CZ.

Schot, P.P. & Molenaar, A. 1992. Regional changes in groundwater flow patterns and effects on groundwater composition. *J. Hydrol*. 130: 151-170.

Schot, P.P., Dekker, S.C. & Poot, A. 2004. The dynamic form of rainwater lenses in drained fens. *J. Hydrol*. 293: 74-84.

Schult, M. 2002. *Durchströmungsmoorgenese am Beispiel des Trebel-Flusstalmoors bei Kirch-Baggendorf*. Diplomarbeit, Botanisches Institut, Universität Greifswald, DE.

Siegel, D.I. & Glaser, P.H. 1987. Groundwater flow in a bog-fen complex, Lost River peatland, northern Minnesota. *J. Ecol*. 75: 743-754.

Sival, F.P., Mücher, H.J. & van Delft, S.P.J. 1998. Management of basiphilous dune slack communities in relation to carbonate accumulation and hydrological conditions. *J. Coastal Conserv*. 4: 91-100.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in North Swedish mire waters. *Oikos* 2: 241-258.

Steiner, G.M. 1992. *Österreichischer Moorschutzkatalog*. Ulrich Moser, Graz, AT.

Stuyfzand, P.J. 1993. *Hydrochemistry and hydrology of the coastal dune area of the Western Netherlands*. Ph.D. Thesis, Free University of Amsterdam, Amsterdam, NL.

Succow, M. 1988. *Landschafsökologische Moorkunde*. VEB Gustav Fischer Verlag, Jena, DE.

Succow, M. & Joosten, H. (eds.) 2001. *Landschafsökologische Moorkunde* (2nd. ed.) Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, DE.

Tóth, J. 1962. A theoretical analysis of groundwater flow in small drainage basins. *J. Geophys. Res*. 68: 4795-4812.

Tyler, C. 1981. Geographical variation in Fennoscandian and Estonion *Schoenus* wetlands. *Vegetatio* 45: 165-182.

van Andel, J. & Arondsen J. (eds.) 2006. *Restoration ecology; The new Frontier*. Blackwell Academic Publishers, Oxford, UK.

van den Hoek, D. 2005. *The effectiveness of restoration measures in species-rich fen meadows*. Ph.D. Thesis Wageningen University, Wageningen, NL.

van Diggelen, R. 1998. *Moving gradients: Assessing restoration prospects of degraded brookvalleys*. Ph.D. Thesis, University of Groningen, Groningen, NL.

van Duren, I.C., Strykstra, R.J., Grootjans, A.P., ter Heerdt, G.N.J. & Pegtel, D.M. 1998. A multidisciplinary evaluation of restoration measures in a degraded fen meadow (*Cirsio-Molinietum*). *Appl. Veg. Sci*. 1: 115-130.

van Wirdum, G. 1991. *Vegetation and hydrology of floating rich-fens*. Ph.D. Thesis, University of Amsterdam, Amsterdam, NL

van Wirdum, G. 1993. An ecosystem approach to base-rich freshwater wetlands, with special reference to fenland. *Hydrobiologia* 265: 129-153.

Wassen, M.J. & Joosten, J.H.J. 1996. In search of a hydrological explanation for vegetation changes along a fen gradient in the Biebrza Upper Basin (Poland). *Vegetatio* 124: 191-209.

Wassen, M.J, Barendregt, A., Pałczyński, A., de Smidt, J.T. & de Mars, H. 1990. The relationship between fen vegetation gradients, groundwater flow and flooding in an undrained valley mire at Biebrza, Poland. *J. Ecol*. 78: 1106-1122.

Wassen, M.J., van Diggelen, R., Verhoeven, J.T.A. & Wołejko, L. 1996. A comparison of fens in natural and artificial landscapes. *Vegetatio* 126: 5-26.

Wassen, M.J., Peeters, W.H.M. & OldeVenterink, H. 2002. Patterns in vegetation, hydrology and nutrient availability in an undisturbed river floodplain in Poland. *Plant Ecol*. 165: 27-43.

Wassen, M.J., Olde Venterink ,H., Lapshina, E.D. & Tanneberger, F. 2005. Endangered plants persist under phosphorus limitation. *Nature* 437: 547-550.

Weber, C.A. 1900. Ueber die Moore, mit besonderer Berücksichtigung der zwischen Unterweser und Unterelbe liegenden. *Jahresber. Männer v. Morgenstern* 3: 3-23.

Weber, C.A. 2002. *On the vegetation and development of the raised bog of Augstumal in the Memel delta*. In: Couwenberg, J. & Joosten, H. (eds.) C.A. Weber and the raised bog of Augstumal – with a translation of the 1902 monograph by Weber. IMCG/PPE 'Friff & K', Tula, RU.

Wheeler, B.D. 1999. Water and plants in freshwater wetlands. In: Baird, A.J. & Wilby, R.L. (eds.) *Eco-hydrology; plants and water in terrestrial and aquatic environments*, pp. 127-180. Routledge, London, UK.

Wołejko, L., Aggenbach, C., van Diggelen, R. & Grootjans, A.P. 1994. Vegetation and hydrology in a spring mire complex in western Pomerania, Poland. *Proc. R. Neth. Acad. Sci*. 97: 219-245.

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