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# The restoration of fens in the Netherlands

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## Abstract

The present paper reviews the major environmental problems in Dutch aquatic and semi-terrestrial fens: desiccation, (internal and external) eutrophication, acidification, habitat fragmentation and intoxication. It discusses both the positive and the negative consequences of the restoration measures taken in Dutch fens, and strongly emphasises the biogeochemical and biological processes and factors responsible for the deterioration of plant and animal communities in fens. Only with the knowledge of these key processes and factors are optimal restoration and management measures possible. Finally, important gaps in knowledge are pointed out and a call for new research is made.

## Introduction

This paper discusses the restoration of Dutch mineral-rich peatlands with either surface or submerged peat accumulation. Although some fens are brackish (8.5–85 mmol Cl $l^{-1}$; mainly in the western part of the Netherlands), the majority are freshwater systems. We focus mainly on aquatic and semi-terrestrial fens (for terrestrial fen meadows, see Grootjans et al., 2002). Fens differ from ombrotrophic mires (bogs) in that the biogeochemical processes in their top layer are strongly influenced by the influx of mineral-rich groundwater or surface water (telluric water) (Gore, 1983; Wheeler & Proctor, 2000). Minerals may be supplied either by vertical flow (groundwater discharge, upward seepage), by horizontal flow (supply of surface water or groundwater) or a combination of both. The assumption that this automatically implies meso- or eutrophic conditions is absolutely incorrect. Studies have shown that mineralisation rates and nutrient availability are not necessarily lower in bog plant communities comparing with fen plant communities. The uptake of nutrients, rather than their availability, appears to form the principal constraint for plant growth in bogs (Waughman, 1980; Verhoeven et al., 1988; Koerselman & Verhoeven, 1992; Aerts et al., 1999). The term 'minerotrophic' strictly refers to the mineral richness (in particular of calcium (Ca) and magnesium (Mg)), whereas 'eutrophic' refers to the high availability of primary nutrients (in particular phosphorus (P), nitrogen (N), and potassium (K), and also carbon (C) for some aquatic systems). The key variables for the distinction between both mire types are, therefore, mineral concentrations, acid neutralising capacity (ANC), and often also pH, all variables being generally higher in fens. The ANC in fens is provided by bicarbonate buffering and by the exchange of base cations (Ca and Mg) against hydrogen ions on cation exchange sites in the peat. For an assessment of the ANC, bicarbonate concentrations, total cation exchange capacity (CEC) and base saturation (BS) are, therefore, important. Buffering by bicarbonate in surface and sediment pore water provides the first and most important mechanism against acidification. When almost all bicarbonate has been consumed, e.g. during desiccation, the pH drops to $<5$ and acids are buffered by cation exchange at binding sites in the soil or sediment. The power of the latter mechanism is determined by the total concentration of cation binding sites (CEC), and the BS, which is the percentage of the CEC occupied by base cations (in equivalents of charge). CEC and BS differ considerably between fen types, and BS is periodically lowered in fens where the water table drops below surface level during summer.

*Figure 1.* This old school print shows a peat-digger piling up peat blocks on the baulk. Note the long and rectilinear fen ditches, from which peat has been dredged from both sides. (Bos & Kwast, Wolters Publish., Groningen, Den Haag.)

## Fens in the Netherlands

In the Netherlands, the nature of minerotrophic peatland areas has been strongly shaped by the extraction of peat, creating a distinctive pattern of turf ponds (called '*petgaten*' in Dutch), and baulks ('*legakkers*') onto which the extracted peat was deposited to dry (Figs 1 and 2). Many dams were blown away by storms, thus creating large shallow lakes called broads ('*wieden*'). Many of the former smaller turbaries got terrestrialised, and the present vegetation is strongly dependent on the type of management (Van Wirdum, 1991; Den Held et al., 1992; Van Wirdum et al., 1992; Wheeler & Shaw, 1995). The typical Dutch peatland type, a semi-natural landscape (Westhoff et al., 1970) created by anthropogenic activity, is comprised of many species-rich plant communities and offers an important habitat to waterfowl. Dutch fens contain many internationally threatened plant communities and species (Vermeer & Joosten, 1992). Like other wetland types, most fen peatlands are under the protection of the National Nature Policy Plan. Due to their unique character, the remaining large fen areas have been recognised as Ramsar Sites, i.e. Wetlands of International Importance. Some sites, such as the National Park *De Weerribben* (Overijssel), were already recognised in 1980 (Frazier, 1999). This stresses the need for conservation and restoration of Dutch fens with high priority, both from a national and international point of view.

Most of the remaining fens in the Netherlands are peatland remnants of the Holocene floodplain, which was once covered by extended mire areas (Pons, 1992). Different successional stages were present, from open water dominated by hydrophytes and helophytes, to floating fens and carr woods. In areas where water was less rich in minerals, like in the contact zones with elevated Pleistocene parts of the country, various types of transitions from fen to bog were present. The characteristic continuum between

*Figure 2.* A satellite image of a fen area near Utrecht clearly shows the rectilinear method of peat extraction, which is characteristic for most Dutch fens. The destruction of peat baulks, mostly by storms, resulted in shallow lakes (dark) like the Vinkeveensche Plassen (left) and Loosdrechtse Plassen (right). European Space Agency (ESA) / National Aerospace Laboratory (NLR). Scale 1:155 000.

fens and bogs has now almost entirely vanished in the Netherlands, largely because of anthropogenic activities (see also Roelofs et al., 2002). Floodplain bogs developed in Holocene areas on locations where the accumulation of peat became elevated above the water level and telluric water could no longer reach the top layer (Pons, 1992; Schultz, 1992). Between 0 AD and 1200–1500 AD, however, these bogs were inundated by the rising sea level and the initiation of agricultural land use (Pons, 1992; van de Ven, 1994; van ‘t Veer et al., 2000). Most of the present fens developed on this drowned bog peat. In areas (formerly) influenced by the sea, like the Northwestern part of the Netherlands, fens developed under brackish conditions. In many Pleistocene areas, small fens developed due to the seepage of calcareous water from higher plateaus, or because of flooding or infiltration of riverine water. At present, small fragments of these peatlands still exist, scattered over the Pleistocene regions. Both in the Holocene lowlands and in the Pleistocene brook valleys, fens also developed on reservoir basins (‘boezems’ in Dutch), used to store excess water during winter. After they lost their storage function, valuable plant communities (fen meadows) developed in these areas flooded in winter.

Almost all recognised fen reserves are in the Holocene part of the Netherlands. Their area ranges between 200 ha and 600 ha, a few reserves being larger 1300–4500 ha (e.g. De Wieden and De Weerribben in Overijssel, Alde Feanen in Friesland). In addition, there are many small fens in both Holocene and Pleistocene areas, generally being up to 10 or 20 ha but still containing an important portion of the plant communities threatened in the Netherlands.

Due to the wide diversity in habitats, both terrestrial and aquatic, and the high availability of food,

*Table 1.* Overview of plant communities occurring in Dutch fens on the alliance level (Schaminée et al., 1995, 1996, 1998; Stortelder et al., 1999)

| Type | ALLIANCE | Some characteristic species |
|---|---|---|
| Open water and watersides in fens (lakes, pools, ditches) | HYDROCHARITION MORSUS-RANAE | *Hydrocharis morsus-ranae, Stratiotes aloides, Lemna* spp. |
| | PARVOPOTAMION | *Potamogeton pusillus, P. trichoides, P. mucronatus, Elodea nutalii* |
| | NYMPHAEION | *Nymphae alba, Nuphar lutea, Nymphoides peltata Potamogeton compressus, P. lucens, Polygonum amphibium,* |
| | ZANICHELLION PEDICELLATAE | *Zanichellia palustris, Ranunculus aquatilis, Ceratophyllum submersum, Ranunculus baudotii* |
| | CHARION FRAGILIS | *Chara contraria, Nitella hyalina* |
| | CHARION VULGARIS | *Chara vulgaris, Elodea nutallii* |
| | RANUNCULION PELTATI | *Ranunculus aquatilis, Callitriche platycarpa, C. hamulata, Potamogeton alpinus* |
| | RUPPION MARITIMAE (only in brackish fens) | *Ruppia cirrhosa, Zanichellia palustris* |
| | LEMNION TRISULCAE | *Lemna trisulca, Riccia fluitans, Ricciocarpos natans, L. minor* |
| Marshes | SPARGANIO-GLYCERION | *Veronica beccabunga, Rorippa nasturtium-aquaticum, Hippuris vulgaris* |
| | CICUTION VIROSAE | *Cicuta virosa, Carex pseudocyperus, C. paniculata, Calla palustris, Lemna* spp. |
| | PHRAGMITION AUSTRALIS | *Phragmites australis, Bolboschoenus (Scirpus) maritimus, Typha latifolia, T. angustifolia, Schoenoplectus (Scirpus) lacustris, Iris pseudacorus*, *Acorus calamus*, *Glyceria maxima, Lemna gibba, L. trisulca, Spirodela polyrhiza* |
| Fens dominated by large sedges | CARICION GRACILIS | *Carex acuta, C. acutiformis, Calliergon cordifolium, Equisetum fluviatile, Iris pseudacorus* |
| | CARICION ELATAE | *Carex elata, C. paniculata, Lysimachia thyrsiflora, Peucedanum palustre, Cladium mariscus* |
| Fens dominated by small sedges | CARICION DAVALLIANAE | *Carex oederi, C. diandra, Parnassia palustris, Epipactis palustris, Dactylorhiza incarnata, Eleocharis quinqueflora, Juncus subnodulosus, Pinguicula vulgaris, Carex pulicaris, Campylium stellatum, Eriophorum gracile, C. polygamum, Scorpidium scorpioides*, in general very rich in mosses and liverworts |
| | CARICION NIGRAE | *Carex nigra, Potentilla palustris, Carex curta, Viola palustris, , Ranunculus flammula, Polytrichum commune, Agrostis canina, Sphagnum palustre, S. fimbriatum, S. subnitens, Aulacomnium palustre* |
| Fen meadows | JUNCO-MOLINION (Litter fen) | *Succisa pratensis, Carex panicea, C. hostiana, Cirsium dissectum, Juncus conglomeratus, Molinia caerulea* |
| | CALTHION PALUSTRIS | *Caltha palustris, Lychnis flos-cuculi, Rhinanthus angustifolius, Dactylorhiza majalis, Lotus uliginosus, Carex disticha* |

| | | |
|---|---|---|
| | FILIPENDULION | *Filipendula ulmaria, Thalictrum flavum, Lythrum salicaria, Lysimachia vulgaris, Valeriana procurrens* |
| | EPILOBION HIRSUTI | *Epilobium hirsutum, Angelica archangelica, Eupatorium cannabinum, Phragmites australis* |
| | BIDENTION TRIPARTITAE | *Bidens cernua, B. tripartita, Rumex palustris, Persicaria hydropiper, P. mitis, P. minor, Alopecuris aequalis* |
| Heavily fertilised pastures | CYNOSURION CRISTATI | *Cynosurus cristatus, Anthoxanthum odoratum, Bellis perennis, Plantago major, Lolium perenne* |
| Streambank communities | FILIPENDULION | *Filipendula ulmaria, Valeriana officinalis, Thalictrum flavum, Leucojum aestivum, Lathyrus palustris* |
| | EPILOBION HIRSUTI | *Sonchus palustris, Epilobium hirsutum, Althaea officinalis, Cochlearia officinalis* ssp. *officinalis, Eupatorium cannabinum* |
| Carrs | SALICION CINEREAE | *Salix aurita, S. cinerea, Frangula alnus, Iris pseudacorus, Lythrum salicaria, Lysimachia vulgaris, Carex acuta, Glyceria maxima* |
| | ALNION GLUTINOSAE | *Alnus glutinosa, Phragmites australis, Iris pseudacorus, Carex paniculata, Carex acutiformis,C. riparia, Thelypteris palustris, Salix cinerea, Peucedanum palustre, Lysimachia thyrsiflora, Ribes nigrum, Caltha palustris, Cardamine amara* |
| | BETULION PUBESCENTIS | *Betula pubescens, Carex curta, Sphagnum squarrosum, Calamagrostis canescens, Phragmites australis, Alnus glutinosa* |
| Bog communities in fens | OXYCOCCO-ERICION (ERICO-SPHAGNION) | *Oxycoccus palustris, Andromeda polifolia, Eriophorum vaginatum, Sphagnum papillosum, S. magellanicum, S. rubellum, Erica tetralix* |

*Table 2.* Examples of animal species characteristic of Dutch fens

| Group | Some characteristic species |
|---|---|
| Mammalia | *Microtus oeconomus* (Northern vole), *Lutra lutra* (Otter), *Neomys fodiens* (European water shrew) |
| Aves | *Area purpurea* (Purple heron), *A. cinerea* (Grey heron), *Botaururus stellaris* (Great bittern), *Phalacrocorax carbo (incl. sinensis)* (Great cormorant), *Platalea leucorodia* (Eurasian spoonbill), *Anser anser* (Greylag goose), *Porzana porzana* (Spotted crake), *Acrocephalus arundinaceus* (Great reed warbler), *A. schoenobaenus* (Sedge warbler), *Locustella luscinioides* (Savi's warbler), *Panurus biarmicus* (Bearded tit), *Remiz pendulinus* (Penduline tit), *Luscinia svecica* (Bluethroat), *Chlidonias niger* (Black tern), *Circus aeruginosus* (Marsh harrier) |
| Amphibia | *Triturus vulgaris* (Common newt), *Rana ridibunda* (Marsh frog), *R.* kl. *esculenta* (Green frog), *R. lessonae* (Pool frog), *R. temporaria* (Common frog), *Bufo bufo* (Common toad), *Hyla arborea* (European tree frog) |
| Reptilia | *Natrix natrix* (Grass snake), *Lacerta vivipera* (Common lizard) |
| Insecta | Lepidoptera: *Lyceana dispar* (Large copper), *Maculinea alcon* (Alcon blue), *Coenonympha tullia* (Large heath), *Clossiana selene* (Small pearl-borderred fritillary)<br>Odonata: *Coenagrion pulchellum, Cordulia aenea, Aeshna viridis, Leucorrhinia pectoralis*<br>Orthoptera: *Chorthippus montanus, Chrysochraon dispar, Stethophyma grossum* |

many different animal species dwell in fens. Fens support a significant portion of the both the numbers and species of waterfowl in the Netherlands (Table 2), There is, therefore, an urgent need to protect and restore these fens. Traditionally, birds have always received most attention, which is the reason why this animal group dominates Table 2. Fens, however, also provide an important habitat to many other sensitive animals including fish, amphibian and macroinvertebrate species (Table 2). A striking example is *Aeshna viridis*, a dragonfly that is found only in peatlands with extensive and healthy *Stratiotes aloides* stands. In contrast to the research on plant communities, only a few studies have focused on fauna communities in fens (e.g. Higler, 1977).

The history of Dutch fens is characterised by peat extraction, land reclamation and hydrological measures. Only when bog peat became scarce did people begin to dredge the inferior fen peat. Economical peat extraction persisted in Dutch fens until the fifties of the twentieth century. For safety reasons and for agricultural purposes, a strong control of the water levels and flows became increasingly necessary throughout the centuries. Dikes, weirs, dams, water basins and pumping stations were used to avoid problems with excess water. Fen peatlands became strongly regulated landscapes controlled by artificial water management. At present, the Netherlands have become so densely populated that it is impossible to consider the management and restoration of fens solely from an ecological viewpoint. Ecological restoration will only be possible within a tight hydrological framework, which is strongly dominated by agricultural interests and public safety.

## Plant communities and site conditions

Fens in the Netherlands contain many different plant communities, including the most species-rich plant communities in the country. An outline of the fen types in the Netherlands, from open water to carr woods and transitions to small bog communities, is summarised in Table 1. Litter from the vegetation provides peat, and peat accumulation in its turn controls succession (Bakker et al., 1997). In small lakes, and in littoral zones of larger water bodies (for the latter, see Gulati & van Donk (2002)), there is a succession from systems dominated by aquatic macrophytes, to floating plant communities or emergent communities of tall helophytes (*Phragmites australis, Typha* spp., *Scirpus* spp.; Fig. 3). Slightly brackish fens, like Ilperveld, contain characteristic plant communities including species like *Ruppia maritima, Chara canescens* and *Schoenoplectus tabernaemontani.* More eutrophic terrestrial sites are dominated by *Althaea officinalis* and *Cochlearia officinalis* ssp. *officinalis*.

The level of nutrient supply strongly determines the composition of the vegetation. High nutrient concentrations, particularly of phosphate ($PO_4^{3-}$), strongly promote the growth of plants possessing floating leaves such as *Lemna* spp., *Nuphar lutea* and *Nymphaea* spp. Submerged macrophytes such as *Potamogeton compressus* and *Chara* spp. and their associated fauna start disappearing at $PO_4^{3-}$ concentrations around 5 $\mu$mol $l^{-1}$ (de Lyon & Roelofs, 1986). Even at higher $PO_4^{3-}$ concentrations (10–20 $\mu$mol $l^{-1}$) high phytoplankton concentrations will develop, or the water becomes completely covered by *Azolla filiculoides*, a fern that can fix N due to its symbiotic relationship with cyanobacteria. Whether higher $PO_4^{3-}$ concentrations actually lead to massive development of algae or cyanobacteria also depends on the grazing activity of zooplankton. Even eutrophic shallow waters may be clear and therefore suitable for submerged plants, provided that a high topdown control by grazing exists (Shapiro et al., 1975; Jeppesen et al., 1990; Scheffer et al., 1993; Gulati & van Donk, 2002). Eutrophic and hypertrophic helophyte zones are characterised by species-poor stands of e.g. *Phragmites australis* and *Glyceria maxima*.

During terrestrialisation, the vegetation development is to a large extent determined by traditional agricultural and water management or, more recently, by nature management. Quaking fens and fen meadows that are annually mown often develop into species-rich areas, characterised by small sedges such as *Carex pulicaris, C. oederi*, *C. lasiocarpa* and *C. diandra,* with a significant cover of mosses such as *Campylium polygamum* and characteristic *Scorpidium* spp. (van Wirdum, 1991; van Wirdum et al., 1992; Schaminée et al., 1995). On locations with a higher nutrient availability, the plant communities are often less species-rich and dominated by *Carex nigra,* or by larger sedges like *C. acuta* or *C. paniculata*. For semi-terrestrial and terrestrial fen plant communities, both P, N and occasionally K (co-)limitation has been reported (Pegtel, 1983; Vermeer, 1986; Koerselman & Verhoeven, 1992; Verhoeven et al., 1996; van Duren et al., 1997). Fertilisation experiments pointed out that in relatively young fens, mown and harvested for 15–20 years, biomass production is generally limited by N. Old fens, with a vegetation that has been mown yearly for over 40 years, tend to be limited by P (Vermeer, 1986; Koerselman & Verhoeven, 1992; Verhoeven et al., 1996). This appears to be caused by an relatively higher removal rate of this nutrient by the collection of hay, as N and K leaching from the litter is much more rapid (Koerselman & Verhoeven, 1992). As the relative availabilities of N and P are reflected in the concentrations of the nutrients in plant tissues, their ratio may be used as an easy instrument to confirm which nutrient is rate-limiting for biomass production (Verhoeven et al., 1996). However, if this information is used for the evaluation of eutrophication effect, one has to note that plant communities may become dominated by one or few species after eutrophication, without changes in the total biomass (Lamers et al., 1999a).

At present, an important anthropogenic source for N is its atmospheric deposition, caused mainly by ammonia emissions by the agricultural activities and nitrogen oxides emissions by the combustion processes (traffic, power plants). The Netherlands has the highest ammonia production rates per unit area in the world because of the intensive animal husbandry. This has resulted in bulk deposition rates averaging 30–40 kg N $ha^{-1}$ $a^{-1}$ (Bobbink et al., 1999), which are roughly up to 2 orders of magnitude higher than the estimates for background level (0.5–5 kg N $ha^{-1}$ $a^{-1}$: Aber et al., 1989). In the 1980s, some parts of the Netherlands even received 80–100 kg N $ha^{-1}$ $a^{-1}$(Houdijk et al., 1991). Therefore, even without active fertilisation or pollution of groundwater or surface water, Dutch fens receive very high N inputs. During recent decades, the airborne N input has even formed the principal N source for fens, even for the fens surrounded by heavily fertilised meadows (Koerselman et al., 1990a). In those fens where biomass production is (co-)limited by N, vegetation responses are expected. The denitrification N loss (averaging 1–2.5 kg $ha^{-1}$ $a^{-1}$) is relatively unimportant in the total N budget. There is only moderate denitrifying activity because ammonium ($NH_4^+$) is the main N species and nitrate ($NO_3^-$) supply is low (Koerselman & Verhoeven, 1992). In fens receiving high $NO_3^-$ loads, e.g. by water runoff from heavily fertilised pastures or corn fields, denitrification rates may be higher (Koops et al., 1996).

Without mowing, most fen types will rapidly develop into reed lands or carr vegetation (Wiegers, 1992). Mature alder carrs are able to fix extremely high amounts of atmospheric N, about 60 kg N $ha^{-1}$ $a^{-1}$with extremes higher than 100 kg N $ha^{-1}$ $a^{-1}$, because of N-fixing nodules in *Alnus* roots formed by the symbiotic actinomycete *Frankia* (Akkermans, 1971). This activity provides a very significant natural N influx. Small alder saplings, often occurring in younger or regularly mown fens, appear to be of minor import-

*Figure 3a–b.* Space for time substitution, caused by time differences between peat excavations, shows the natural succession during terrestrialisation in the same small fen ditch. Without management, *Stratiotes aloides* stands (a) are succeeded by floating fens dominated by tall helophytes including sedges (b), which in turn develop into carr (c).

ance in the natural N budget (Koerselman et al., 1989). Carrs provide a habitat to many mycorrhizal fungi, including several rare species (Arnolds et al., 1995). Their role in nutrient acquirement and system functioning is, however, largely unknown (J. Baar, pers. com.).

*Figure 3c.*

The locations of many fen plant communities, like *Calthion palustris, Alnion glutinosae* and *Caricion davallianae* are characterised by groundwater that is not only rich in Ca and Mg, but also in Fe. The essentially chemical oxidation of Fe facilitated by the anaerobic groundwater produces rusty sites, with patches of oil-like films of Fe-oxidising bacteria and their products. On sites where the influence of minerals is fading because of vertical and/or horizontal isolation from telluric water, *Sphagnum* hummocks may develop into small bog communities (*Oxycocco-Ericion*).

Apart from water composition, the extent and timing of water level fluctuations strongly determine vegetation development. Litter fens (*Junco-Molinion* communities) only develop on haylands that show moderate desiccation of the topsoil during the summer. Permanently waterlogged conditions will automatically lead to plant communities characterised by small sedges.

## Deterioration of fens

The primary cause for the loss and degradation of fens is desiccation caused by drainage. Land reclamation, the construction of numerous channels and ditches, and the lowering of surface water levels and groundwater tables lead to the severe desiccation of wetlands. In many wetlands, groundwater tables have dropped from a few decimetres to up to >1 m in the recent decades. In most Dutch fens, water tables and often also surface levels of the surrounding area are up to 1m lower than the fen reserve. This is caused by water management measures and peat settlement, leading to irreversible hydrological changes. As a consequence, most fens have changed from upward seepage areas or hydrologically neutral areas to (net) infiltration areas. This has not only caused direct desiccation problems because of the decrease of soil moisture supply to the vegetation, but also has induced indirect biogeochemical problems. As fen vegetation depends on mineral supply from telluric water, a decrease of the water table will mostly lead to lower concentrations of bicarbonates, carbonates, Ca and BS, and therefore to a decrease in the ANC. The influence of calcareous water declines and the top layer becomes increasingly dominated by rainwater (van Wirdum, 1991; Wassen & Barendregt, 1992; Beltman et al., 1996ab). Due to the loss of ANC, pH may drop from values from 6–6.5 to 4. This is indicated by the decrease or disappearance of characteristic fen mosses like *Scorpidium scorpioides* and the strong increase of moss species like *Polytrichum commune*, *Sphagnum squarrosum, S. subnitens* and *S. recurvum* (Beltman et al., 1995; Kooijman & Bakker, 1995). *Sphagnum* contributes to the acidification by active cation ion exchange, and decreases decomposition rates due to the excretion of allelopathic monophenolics (Verhoeven & Liefveld,

*Figure 4.* The use of allochthonous water to maintain high water tables during summer caused eutrophication in this peat extraction pond. Filamentous algae dominate, while some *Stratiotes aloides* plants can barely persist (inlay). Photo L. Lamers.

1997). Moreover, desiccation itself generates acidification through the chemical oxidation of Fe and sulphide, generating sulphuric acid (Lamers et al., 1998a). The drop of the pH to values around 4 leads to an enormous increase in the mobility of potentially toxic metals, including heavy metals in the soil. The aluminium concentrations measured in acidified areas are shown to be toxic to rare species in litter fens (e.g. *Cirsium dissectum*). This toxicity can be counteracted by simultaneously raised Ca concentrations (de Graaf et al., 1997). The effect of desiccation or isolation is therefore twofold: a decrease of the pH (and concomitant increased 'free' metal concentrations) and a decrease of the concentration of detoxifying Ca. A hydrological problem specific to brackish fens is desalinisation, caused by altered agricultural water management and by the damming of the former Zuiderzee by the Aflsluitdijk, which has converted the inland sea into a freshwater lake. As a result of this, the chloride concentrations have dropped below 28 mmol $Cl^- l^{-1}$, a value considered to be the minimum for brackish fen development (R. van 't Veer, pers. com.).

In freshwater fens, however, acidification is not the only reason for undesired species replacement. *Scorpidium scorpioides* is, for instance, quite capable of surviving and growing under mineral-poor conditions. Nutrient availability is also an important determinant of the direction of vegetation changes. *Sphagnum squarrosum*, for instance, can efficiently utilise nutrients in eutrophic environments, making high growth rates possible. In species replacement, therefore, both water quality changes and interspecific competition seem to be involved (Kooijman & Bakker, 1995). Similar changes, generally regarded as problems, are also caused by the isolation from mineral-rich surface water. This isolation may, however, be caused by both anthropogenic and natural processes. As with desiccation, the minerotrophic vegetation loses the supply of vital minerals and, concomitantly, soil ANC decreases.

Desiccation may stimulate decomposition and mineralisation. Grootjans et al.(1986) have shown that the N availability increased due to long-term desiccation. In contrast, the P availability decreases because the capacity of the soil or sediment to bind P strongly increases during desiccation due to the oxidation of Fe. These opposing effects of drought on the availability of both nutrients, in addition to direct drought effects, cause adverse shifts in the vegetation composition. Characteristic sedges disappear and grasses like

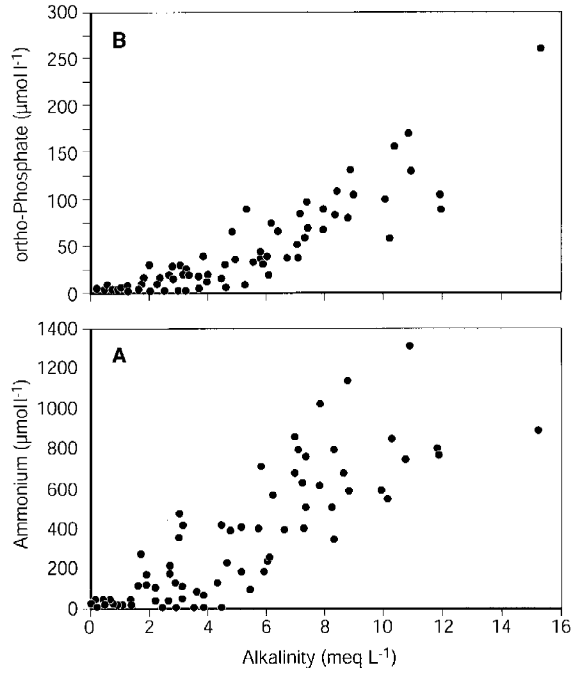

*Figure 5.* Relationship between alkalinity and (A) $NH_4^+$ or (B) $PO_4^{3-}$ concentrations in sediment pore water for 70 randomly selected fen sediments in the Netherlands. From: Smolders 1995.

*Holcus lanatus* and *Agrostis canina* take over (Grootjans et al., 1986). Acidification during desiccation, e.g. by the oxidation of iron sulphides can, however, tone down or even nullify this stimulation of decomposition and mineralisation (Lamers, 2001).

The eutrophication of surface and/or groundwater poses another severe threat to fens. Nutrient influx from agricultural areas and sewage has led to a strong increase of $PO_4^{3-}$ and $NO_3^-$ availability. To compensate for the shortage of water in nature reserves and agricultural areas, water from the rivers Rhine and Meuse is (directly or indirectly) used on a large scale (Roelofs, 1991). Aquatic communities lose their submerged plants and become dominated by fast growing, lemnid species and macro-algae (Fig. 4). Thus, vast fen areas (ditches, pools, lakes) show a strong decline of their biodiversity and change into species-poor plant communities. Likewise, (semi-) terrestrial fens loose many species. Highly competitive species like *Glyceria maxima*, *G. fluitans, Phragmites australis* and *Schoenoplectus (Scirpus) lacustris* become dominant. This type of eutrophication, in which nutrients are imported, is termed 'external eutrophication' to distinguish it from 'internal eutrophication' caused by internal mobilisation of nutrients. The latter has also been reported to lead to fen deterioration. Water shortage in Dutch fen peatlands is generally offset by the use of riverine water, having a higher net alkalinity. In fens containing moderately buffered peat, the influx of alkaline surface water has been shown to increase the decomposition of organic matter, by neutralising the organic acids in organic particles (McKinley & Vestal, 1982; Brock et al., 1985; Kok & van de Laar, 1991; Smolders, 1995; Brouwer et al., 1999). Thus, overall mineralisation is stimulated, leading to eutrophication. In most fens, the stimulating effect of Ca (as bicarbonates and carbonates) on decomposition and consequently on P-mineralisation appears to completely nullify any possible effects of Ca on P binding, at the pH prevailing (Fig. 5; Roelofs, 1991; Smolders, 1995; Brouwer et al., 1999).

Moreover, river waters are characterised by relatively high concentrations of sulphate because of natural weathering of sulphate containing rocks, anthropogenic dumping and sulphur runoff from agricultural areas. Groundwater and surface water are sulphate-enriched by desiccation and by $NO_3^-$ pollution. In the first process, sulphate is mobilised from iron sulphide ($FeS_x$) deposits by oxidation and, in the second, $NO_3^-$ is used by denitrifiers to oxidise sulphides to sulphate (Lamers et al., 1998a, 1999a). In freshwater systems, microbial sulphate reduction is generally limited by the availability of sulphate. Increased sulphate concentrations in fens will, therefore, stimulate sulphate reduction. As the consumption of organic acids is accelerated, overall decomposition will also be stimulated. In addition, the sulphide formation resulting from sulphate reduction generates alkalinity, stimulating the decomposition further (as explained above). The sulphide formed binds to iron (hydr)oxides in the sediment forming iron sulphides such as $FeS_2$ (pyrite) and FeS. As a result, $PO_4^{3-}$, the major limiting nutrient, is released from Fe~P compounds and diffuses into pore and surface water (Boström et al., 1982; Caraco et al., 1989; Roelofs, 1991; Smolders & Roelofs, 1993, 1995; Koerselman & Verhoeven, 1995; Lamers et al., 1998b; Beltman et al., 2000) (Fig. 6). This sulphate-driven internal eutrophication is a general process in systems that are limited in energetically more favourable electron acceptors, like oxygen and $NO_3^-$. Therefore, sulphate pollution of groundwater also leads to eutrophication in waterlogged or flooded fen meadows (Jansen & Roelofs, 1996; Lamers et al., 1998b). The response appears to be regulated by the availability of readily decomposable organic matter, indicated by the peat profile (Kemmers, 1996).

Particularly those fens rich in easily decomposable peat will suffer from internal eutrophication due to alkaline, sulphate-enriched water. For understanding the eutrophication-related deterioration of fens, it is essential to recognise both the internal and external sources of nutrient enrichment. In many cases, the increase in concentration of $PO_4^{3-}$ due to accelerated mineralisation appears to be much higher than the $PO_4^{3-}$ concentration of the inflowing waters (Koerselman & Verhoeven, 1995). Reducing the $PO_4^{3-}$ influx, for instance, by chemical stripping of the nutrient (dephosphatising) or by flow through a constructed wetland or an extended supply route, is in this case insufficient to prevent eutrophication.

Nutrient availability in fens is in several ways linked to pH, both biologically and chemically. Increasing the alkalinity and the pH will, as explained above, stimulate decomposition and mineralisation in slightly acidic fens. The chemical binding of $PO_4^{3-}$ is closely related to the pH of the peat. The binding of $PO_4^{3-}$ to Fe and aluminium is strongest at pH values around 6. Binding to calcium as $CaHPO_4$ (optimum at pH 7–8) is of lesser importance, but the binding of $PO_4^{3-}$ as apatite ($Ca_{10}(PO_4)_6(OH)_2$) strongly increases above pH 6.5–7 (Stumm & Morgan, 1981). When pH decreases to about 4.5, $PO_4^{3-}$-binding stays more or less equal, but a decrease in the pH to 4 or less will dissolve metal phosphates (in the Dutch fens mainly Fe$\sim$P) and increase P availability. At the same time, free $NH_4^+$ concentrations increase due to exchange with protons at cation exchange sites in the peat. Therefore, the chemical nutrient binding capacity in fens will change significantly only at pH $<4$ or at pH $>7$. Indeed, Beltman et al. (1996a) found that both N and P-availabilities in fens abruptly increased below pH 4.1.

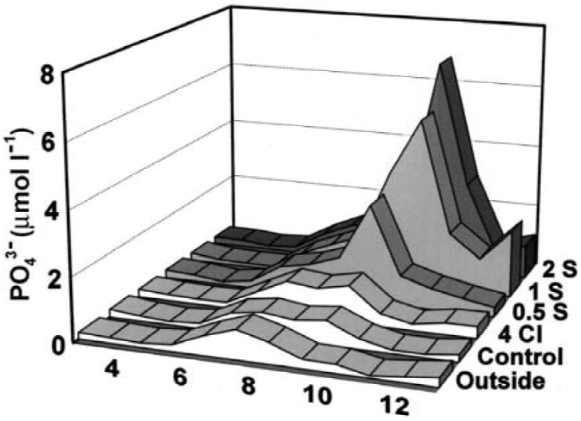

*Figure 6.* Enclosure experiment in a fen ditch, in which either 4 mmol l$^{-1}$ chloride (4 Cl), 0.5 mmol l$^{-1}$ sulphate (0.5 S), 1 mmol l$^{-1}$ sulphate (1 S), or 2 mmol l$^{-1}$ sulphate (2S) has been added to the surface water. All sulphate treatments cause P eutrophication of the surface water (vertical axis), while the control enclosures (Control) and chloride treatment show the normal development of the P concentration throughout the year as measured outside the enclosures (Outside).

A much less known causal factor for the severe deterioration of fens is the enforcement of highly stable water levels. In more natural situations, as in the past, water levels fluctuated throughout the year, being lower in the summer and higher during winter. Current water level regimes in the Netherlands tend to be the opposite: lower winter levels to enable rapid runoff of access water from agricultural land, and relatively high and stable summer levels provide water for growth and evapo-transpiration. In most cases, this unnaturally high summer level can only be maintained when allochthonous river water is used. As stated earlier, this may often lead to internal eutrophication because of enrichment with bicarbonate and sulphate. Another problem that is caused during the high water level is mobilisation of $PO_4^{3-}$ Fe$\sim$P compounds when oxygen becomes depleted and Fe is reduced. Temporal lowering of the water table, which is natural for summer, leads to the oxidation of a greater part of Fe and concomitant stronger $PO_4^{3-}$ binding. In carrs where the water table is raised and artificially maintained high during summer, $PO_4^{3-}$ concentration increase considerably. This leads to a complete domination of the vegetation by *Lemna* spp., at the expense of the original vegetation (A. Boxman & E. Lucassen, pers. com.). In contrast, high water tables during winter will not lead to internal eutrophication, because of the lower microbial activity in winter. Although the hydrology of many fens in the Netherlands has always been a consequence of human activity, we plead for applying a more natural water table management in fens: somewhat lower water tables during summer and higher tables during winter. An additional advantage is the improved conditions (oxygen and light; pers. obs.; Coops & van der Velde, 1995) for germination of submerged plants and helophytes. Whether or not this more natural regime is feasible, will depend on the plant communities involved and hydrological considerations other than nature management. A potential risk of water table reduction seems to be the effect on mineralisation rates. Although constant long-term desiccation (several years) may indeed lead to increased availability of N but not of P (Grootjans et al., 1986; Berendse et al., 1994; Oomes et al., 1997), short-term lowering of the water table (months) in fen peat showed hardly any effect on N availability (Lamers, 2001). Moreover, Oomes et al. (1997) found increased N mineralisation only after 2 years of constantly lowered water table (30 cm below surface level) in fen soils. The application of a more natural hydrological regime in the management of fens requires, however, further research.

In addition, the increase of phytotoxic compounds have apparently become increasingly important in the malfunctioning of fens. Free sulphide ($H_2S$, $HS^-$, $S^{2-}$) is one of the most important biogenic phytotoxins (Koch et al., 1990) and its concentrations have invariably increased due to sulphur pollution in freshwater fens. Even low levels of sulphide harm the roots of *Statiotes aloides* (Smolders & Roelofs, 1996) and decrease the biomass of e.g. *Carex* spp (Lamers et al., 1998b). The competitive advantage of sulphide-resistant, fast growing species will, therefore, increase considerably. Field observations suggest that this may stimulate the formation of monotonous stands of species like *Glyceria maxima*. Free Fe, capable of sequestering toxic sulphide by the formation of iron sulphides, is an important modifier of the sulphide toxicity (Smolders et al., 1995). Loss of groundwater discharge rich in Fe due to desiccation may lead to sulphide toxicity. On the other hand, free Fe, abundant in fens that receive anaerobic groundwater, may itself be toxic to non-characteristic fen plants (Lucassen et al., 2000). Some fen communities, therefore, seem to be governed by toxicity rather than by nutrient availability.

The decline of fen-dwelling fauna has to be attributed to biotope destruction, eutrophication, habitat fragmentation and even toxification (e.g. pesticides and heavy metals). This not only applies to mammals like *Lutra lutra* (Otter) and *Microtus oeconomus* (Northern vole), but also to characteristic birds like *Acrocephalus arundinaceus* (Great reed warbler) and *Botaurus stellaris* (Bittern) (Jefferies, 1988; Kruuk, 1995; van Turnhout & Hagemeijer, 2001). Both bird species, for instance, need extensive *Phragmites australis* zones along fen waters as a habitat. There has, however, been a strong decline of *Phragmites* in recent decades (van der Putten, 1997). Butterflies, such as *Lycaena dispar* (Large copper) and *Clossiana selene* (small pearl-bordered fritillary) depend on very specific vegetation structures within their habitat range, where host plants not only offer opportunities for feeding, but also for oviposition and shelter (Bink, 1992). Extended floating vegetation of *Stratiotes aloides* is needed by the dragonfly *Aeshna viridis* (Green hawker) for oviposition, and the strong decline of this species has been attributed to the decline of healthy populations of its host plant (Higler, 1977). In addition to the above changes, eutrophication of surface waters has also had a negative impact on food availability (e.g. macrofauna) for several bird species and other carnivorous species (van Turnhout & Hagemeijer, 2001). In conclusion, the decline of fen-dwelling fauna has been caused by the strong decline of fen area in the Netherlands and its fragmentation. Plant communities and vegetation structure have become unfit for critical species, and the deterioration of water and sediment quality has had both direct (toxicity) and indirect negative effects (food quantity and quality).

## Restoration objectives

In all cases, restoration aims at the recovery of original plant communities and their fauna, often semi-natural, as known from the times before undesirable anthropogenic disturbances such as desiccation or eutrophication. Restoration should, as Grootjans & van Diggelen (1995) stated, ‘be aimed at restoring the fen system, not at “restoring” fen species’. Note that restorers do not use a ‘pre-human’ concept for most fen types, but rather a cultural-historical concept, using the landscape of the 19th century or the beginning of the 20th century as a benchmark. The idea that not only (so-called) natural, but also semi-natural systems in the Netherlands are well worth conserving, was initiated by Westhoff in 1945. The concept implies the re-establishment of traditional management. This type of restoration, in which vegetation redevelopment forms the main objective, can be termed renaturation (Wheeler & Shaw, 1995). The restoration of peat accumulation, i.e. a ‘true’ system restoration approach (regeneration), is generally not the main goal, but will often be achieved through vegetation development. If, however, restoration implies resetting the (natural) succession, e.g. by sod cutting, restoration will even counteract regeneration.

As desiccation is often the principal cause for the decline of fens, it is not surprising that efforts to recover these systems generally begin with the restoration of the ‘original’ hydrology. ‘Original’ generally refers to the conditions thought to be optimal for the restoration of the *desired* plant communities. Which communities are considered *desired* depends not only on historical frames, but often also on the chosen restoration target. This may even lead to conflicts, e.g. between botanists and bird conservationists, as both groups do not always strive for the same restoration goals. Monotonous reed stands or *Salix* shrubs can be very valuable for the restoration of bird populations, but generally not from a vegetation perspective (Wheeler & Shaw, 1995).

Water quality is just as important as the appropriate water quantity and level. Most fens require a certain mineral enrichment, and the groundwater or surface water supply of these areas should provide the systems with adequate buffering against acidification. The level of buffering has to be very precise, as changes in ANC will lead to changes in the vegetation. In addition, the nutrient flux (determined by nutrient concentration and water flux) should be within the ranges required by the vegetation concerned. For submerged plant communities, it needs to be ensured that the water quality enables appropriate light conditions. The complete coverage of the water surface with floating-leaved species or the massive development of algae in eutrophic fens will obstruct all light. It follows that while hydrological restoration is possible, high nutrient runoff from arable land makes it difficult to restore a fen. As stated above, the recovery of flow of anoxic water that carries Fe might be an additional prerequisite for the recovery of carrs and other fen types. In general, it is easier to restore the local hydrological systems than the regional systems, because in the latter case large areas of land and therefore many different parties are involved. In the Netherlands with its extremely intensive forms of land use, it is almost always an arduous task to raise groundwater tables in the surrounding agricultural areas.

In eutrophied fens, it is essential that the nutrient concentrations of the inflowing surface water or groundwater are minimised so as to combat eutrophication. Internal eutrophication can be alleviated by employing hydrological alternative for the allochthonous, alkaline and sulphate-enriched river water. In (semi-)terrestrial fens that have been heavily fertilised in the past, it may even be necessary to remove the strongly eutrophied top layer, in order to expose the deeper and cleaner peat layers as a substratum for fen vegetation. High concentrations of toxic metals in the soils and sediments will strongly increase the costs of these measures.

In summary, fen restoration aims at the recovery and conservation of characteristic, often semi-natural fen systems (flora and fauna), by restoring the hydrology, hydrochemistry and the sediment considered optimal for the fens under restoration.

## Successful restoration

For the development of submerged plant communities, dominated by Characeae, clear water is an essential requisite. This condition may be achieved via a bottom-up approach, leading to a significant reduction of the nutrient availability, or alternatively by a more top-down oriented approach like biomanipulation (Shapiro et al., 1975; Jeppesen et al., 1990; Scheffer et al., 1993; Hosper, 1997; Gulati & van Donk, 2002). The bottom-up approach will be discussed below. Biomanipulation is defined as the deliberate exploitation of the interactions between components of the aquatic ecosystem, in order to reduce the algal biomass (Shapiro et al., 1975). The main aim is to increase zooplankton (mainly larger-bodied *Daphnia* spp.) grazing on phytoplankton and concomitantly change the turbid- water state to an alternative clear-water state, even though the nutrient concentrations are similar (Scheffer et al., 1993). To achieve this, the system has to be 'pushed' through the hysteresis effect that prevents an easy transition from one state to the other. Once a submerged vegetation has established, it helps to maintain the clear-water equilibrium by providing a habitat for zooplankton, preventing resuspension of sediment particles, competing with algae for nutrients and depressing algal growth by the excretion of allelopathic substances (Scheffer et al., 1993; van Donk & van de Bund, 2002). In many shallow lakes, the desired change to clear water has been achieved by a drastic reduction of the planktivorous and benthivorous fish stocks (Shapiro et al., 1975; see several papers in Gulati et al., 1990; Jeppesen et al., 1990; Moss, 1998; Meijer et al., 1999; Gulati & van Donk, 2002). This amounts to a reduction in the standing crops of planktivorous and benthivorous fish to 10–15 kg $ha^{-1}$ and 15–25 kg $ha^{-1}$, respectively (generally corresponding to a minimal reduction of 75%). In addition, piscivorous fish as *Esox lucius* (Northern pike) and *Stizostedion lucioperca* (Pikeperch) may be (re-)introduced. In smaller turbaries and fen lakes, however, biomanipulation in surface waters of fens and marshes appeared to be far less successful compared with other waters in the Netherlands (Meijer et al., 1999; Meijer, 2000). Only in a few cases, as in lake Duinigermeer (Overijssel), a clear-water equilibrium could be established. In this lake, extensive

*Chara* communities developed after removing about 75% of the fish stock. In a few other fen lakes, the decrease in turbidity proved to be insufficient for colonisation by submerged plants. The causes for failures of biomanipulation as a restoration technique, some of these specific to peatlands, will be discussed in the next section ('Failures').

Unlike aquatic fen communities, (semi-)terrestrial fens are generally threatened by acidification. When the groundwater tables and fluctuations characteristic for the plant communities concerned can be restored, the restoration of acidified fen meadows is often very successful (de Graaf et al., 1994; Jansen et al., 1996; Grootjans et al., 2001). This implies the 'recharge' of the CEC in the rhizosphere with base cations like Ca during the winter, restoring the base saturation and thus the acid neutralising capacity. Litter fens, for instance, recovered when groundwater could reach the rhizosphere again during winter and early spring. When the locations were strongly dominated by graminoids due to eutrophication, sod-cutting (5–10 cm depth) was necessary in order to remove excess nutrients and create chances for the diaspore bank (de Graaf et al., 1994; Jansen & Roelofs, 1996; Jansen et al., 1996; Grootjans et al., 2001). Fast growing, highly competitive graminoids, as *Holcus lanatus, Elymus repens* and *Calamagrostis canescens*, are removed by this measure, and already after one year, characteristic and endangered species like *Cirsium dissectum*, *Parnassia palustris* and *Pinguicula vulgaris* may return. A prerequisite, however, is the occurrence of moderate desiccation of the top layer during summer. The accumulation of $NH_4^+$ under anaerobic conditions seems to cause problems for species such as *Cirsium dissectum* that prefer $NO_3^-$ as N source (Jansen & Roelofs, 1996; de Graaf et al., 1998).

In fen meadows on mineral soils that only suffered from eutrophication, sod cutting proved to be an adequate restoration measure. If acidification is also a concern, restoration will only be successful if measures are taken to restore the ANC of the top layer. The same processes hold for floating fens, in which sod removal leads to a significant reduction of the availability of both N and P (Beltman et al., 1996ab; Fig. 7). Mineralisation rates for both these nutrients showed the same pattern. However, to prevent rapid re-growth of an undesired *Sphagnum-Polytrichum* carpet after a few years, it appeared necessary to construct a small drainage ditch to remove excessive rainwater. This method corresponds with the restoration of ANC by hydrological management in litter fens and other semi-terrestrial fen types. Loss of ANC due to the isolation from telluric water has been successfully combated by this renewed access to the floating peat of base-rich water, for instance in Ilperveld (N-Holland; brackish fen) and in Westbroek (Utrecht; freshwater fen). However, the construction of small ditches through floating peat is only effective for renewed 'mineral reload' if there is a relatively dense network, accompanied by the construction of shallow trenches to remove excess rainwater (Bootsma, 2000). Contrary to the general assumption, the rainwater is barely or not acidic in the Netherlands (due to the high ammonia emission rates), and the acidifying effect of extra nitrification is minimal in the buffered fens. The greatest problem is that the rainwater body on top of the telluric water mass prevents the efficient infiltration of base-rich water to the top layer of the peat. The re-establishment of base-rich water infiltration can only succeed if the intruding water does not contain or generate high nutrient concentrations in the rhizosphere.

The direct application of lime to offset the acidification appeared adequate in restoring alkalinity and pH, but only if the topsoil were removed (Bootsma, 2000). However, base saturation did not increase. Liming without sod-cutting showed no effect on alkalinity or pH, because of rapid reacidification due to the *Sphagnum* mat. Given the expensive and complicated nature of sod cutting, trench digging, or liming, or both, it is unlikely that these measures will be applied to large deteriorated fens. The only alternatives seem to either allow flooding (which is impossible for floating fens) or allow a succession towards more ombrotrophic plant communities or carr woods. Flooding of fen systems may be an appropriate measure to keep the ANC high enough, although the intrusion of surface water into the peat often appeared to be too shallow for sufficient recharge of the base saturation (Vermeer & Joosten, 1992; De Mars et al., 1996; Beltman et al., 2000). It, however, is accompanied by the high risk of (internal) eutrophication. This risk is expected to be low if the intruding water is mesotrophic and does not lead to internal eutrophication, or if a broad buffer zone ('natural helophyte filter') is present, like for instance in Polish river fens. Fens that have developed in the past in flooded areas can only have become mesotrophic under one or both of these conditions. At present, however, most Dutch fens are small fragments fed by alkaline, eutrophic surface water, which generally contains much higher concentrations of $SO_4^{2-}$, leading to internal eutrophication. The experience with a successful restoration of mesotrophic,

*Figure 7.* Restoration of quagfen vegetation by the mechanical removal of the top layer. In this way, succession is reset. Photo: B. Beltman.

semi-terrestrial fen ecosystems on thick peat layers is, however, still limited, and therefore more work is needed.

Eutrophication caused by external nutrient loading can only be prevented by reducing the concentrations of the influx water, or by using a less nutrient-rich water source. The former can be achieved by chemical removal of nutrients (e.g. $PO_4^{3-}$-stripping using Fe compounds) or by biological removal with helophyte filters. In many cases, however, this is not enough to prevent further eutrophication. High bicarbonate and sulphate levels in the influx water promote internal eutrophication in fens, fen lakes and ditches. Strong preference is therefore given to the restoration of the former hydrology, i.e. with reduced use of allochthonous water and wherever feasible by amelioration of groundwater seepage. This may be achieved by establishing a more natural water-table regime (see below) and if possible by increasing water tables in the environs. For lakes with high $PO_4^{3-}$ loading rates from the peaty sediment to the water layer, it may even be necessary to partly or wholly remove this nutrient source by dredging (compare restoration measures for heathland pools: Roelofs et al., 2002). This has been carried out in fen lakes, e.g. Molenpolder near Utrecht.

The addition of Fe to sediments in order to bind $PO_4^{3-}$ shows a strong de-eutrophication effect in both lakes with mineral sediment (Boers, 1991) and in fens (De Bruuk in Gelderland; Smolders et al., 1995). If, however, there is a constant supply of $SO_4^{2-}$ enriched water, the response is only transient because Fe consumption is extremely high. In such a case, Fe addition would both be very laborious and costly and therefore not recommended as a general, large-scale restoration measure (Smolders et al., 1995). The addition of lime in order to bind phosphate will not be effective, because of the strong stimulation of P mineralisation in fen peat (see above), counteracting the possible effect of chemical binding of P (Roelofs, 1991; Smolders, 1995).

In fens that have become terrestrialised to a eutrophic Alder carr or reed vegetation, efforts have been made to restore species-rich, earlier successional stages by renewed peat removal. The Dutch State Forestry Service has even developed a boat specially designed to create new peat holes (Fig. 8). The conversion of carr to open water is, however, the most expensive measure employed in fens, amounting to euro 11 000 per ha. Given the period needed for succession to semi-terrestrial vegetation (20–30 years;

*Figure 8.* The '*Kraggenvreter*' ('Scragh Wolf'), a floating device developed by the State Forestry Service to create new peat holes in fen peatlands. Peat including its vegetation is removed by the machine's harvester arm, mixed with water and piped to a depot. Inlay: the wolf's head (harvester arm) busy under water. Photo: L. Brouwer, State Forestry Department De Weerribben.

Bakker et al., 1994), however, this measure is fairly cheap compared with the costs of annual mowing and harvesting.

On the fertilised meadows acquired by nature conservation agencies or by the state, by temporarily keeping the water level low, basins were (re)created using draglines and bulldozers. After refilling with water, succession began again within a few years with aquaphyte- and helophyte communities (Vermeer & Joosten, 1992; van den Broek & Beltman, 1995; Beltman et al., 1996). It is, however, not clear whether the conditions are appropriate for the formation of mesotrophic floating fens. In many case, eutrophication due to nutrient influx from the present or former agricultural land, or by rapid nutrient mobilisation from the sediment, impedes succession towards this type of mesotrophic fens.

For plant communities that require human interference (mostly mowing), nature management needs to mimic the cultural activities that were once common in these types of peatlands. The other, relatively less expensive, possibility is to leave it to nature and allow succession towards plant communities that are often, but not always, considered less interesting by botanists. The rather monotonous plant communities as *Phragmites australis* stands or *Salix* shrubs can be very important habitat for wetland fauna like waterfowl. In Westbroek (Utrecht) *Salix* fens have been conserved to protect nesting facilities for *Luscinia svecica* (Bluethroat), whereas *Alnus* trees have been removed.

Although the restoration of the original (semi-natural) hydrology, both at the landscape level and at the habitat level is preferred, a more artificial hydrological system may also provide suitable conditions in some situations for which this option is not possible (Boeye et al., 1995; Wassen et al., 1996). An example of this is the seepage of canal water through a bank to the adjacent peatland. In brackish fens, restoration of the original hydrology refers to the recovery of brackish water influx, which is generally hampered by the agricultural use of adjacent land.

A rather new viewpoint is to consider the development of bog vegetation in fens by natural succession, like in some floating fens of De Stobbenribben (Overijssel; G. van Wirdum, pers. com.; Schouwenaars et al., 1997). The traditional viewpoint was to see this vegetation development as undesirable, and to counter it by mowing and *Sphagnum* removal and by digging new ditches to allow the infiltration of telluric water. The development might erroneously be interpreted as anthropogenic acidification, caused by the high input of acidifying deposition. Unlike acid-sensitive ecosystems (e.g. heaths, moorland pools), fens have a high

ANC that is constantly or regularly 'recharged', and the development of acidophilic plant communities often reflects a natural isolation from telluric water. It has become clear that characteristic hummock-hollow communities in fens develop much faster than in many (expensive) restoration projects on cutover bogs. A new hypothesis concerning this rapid development is the supply of carbon dioxide from deeper peat layers, which is much higher in peat influenced by calcareous water (Lamers et al., 1999b). This may induce the rapid formation of *Sphagnum* hummocks because the growth appears to be C (co-)limited.

Until now, hardly any research has focused on the restoration of fauna populations. A rule of thumb for the optimal development of fen fauna seems to rests on a differentiated and diverse type of landscape, providing different habitats for all different animal groups (see above; H. Esselink, pers. com.). Fen restoration has, however, in most cases only focused on the restoration of plant communities, rather than on the restoration of animal groups and their food webs. In order to ensure an ecosystem approach, future research should pay more attention to both plant and animal communities and foodweb aspects.

## Failures

Unfortunately, the cases of literature reporting restoration failures are (for obvious reasons) scarce. In contrast to other lake types, the reduction of turbidity in fen lakes by external or internal measures appeared to be often unsuccessful. Water remained turbid or became turbid again quickly after taking the measures, and submerged plant communities did not develop. In hypertrophic lakes, turbidity is the only possible stable situation. Biomanipulation will only work after $PO_4{}^{3-}$ concentrations are reduced to a concentration range in which two alternative stable states are possible (Scheffer et al., 1993). The threshold value seems to be around 7 $\mu$mol total P $l^{-1}$, although shallow lakes may become clear even at much higher concentrations (Jeppesen et al., 1990; Klinge et al., 1995). This can be attributed to the strong competition of submerged macrophytes with phytoplankton for P, as explained earlier. Poor success with biomanipulation in fens well within the range of two alternative stable states is often caused by insufficient reduction of the fish stock, or by massive fish remigration from small interconnected ditches or through fish exclosures (Meijer, 2000). Especially in fens comprised of a large network of interconnected peat excavation pools and ditches (which is the general peat excavation pattern in the Netherlands), this is expected to become a problem. So far, however, no information is available on these fen types. In large lakes, resuspension of sediment by wind action may induce turbidity; this particularly holds for lakes with peaty sediments. Finally, mass development of cyanobacteria like *Plankthiotrix* spp. in hypertrophic waters might hamper restoration, because they can form inedible and toxic colonies that complicate grazing by *Daphnia* (Gliwicz, 1990; Laurén-Määttä et al., 1997). Also lumping of the filaments will interefere with their grazing by *Daphnia* spp., in addition to their poor food value for the growth of the daphnids (Gulati & van Donk, 2002). Only individual cyanobacteria and small colonies can be, however, consumed by *Daphnia*, in contrast to larger colonies (E. Van Donk, pers. com.). In the evaluation of biomanipulation projects in the Netherlands (Meijer, 2000), however, evidence collected for the edibility, or to the contrary, of these filaments by the daphnids is inadequate (R.D. Gulati, pers. com.).

A major problem in Dutch fens is the fact that terrestrialisation of open water rarely occurs (Verhoeven & Bobbink, 2001). In hypertrophic waters, the low density of macrophytes most likely hampers peat formation. However, in mesotrophic and eutrophic waters the absence of succession towards terrestrial fens remains unclear probably because the rate of peat formation in open water is low. Peat formation rates in the aquatic phase and in floating mats in fens near Utrecht (Molenpolder and Westbroek) were one-quarter to one-half, respectively, of those in semi-terrestrial fens (1 kg $m^{-2}$ $yr^{-1}$; Bakker et al., 1997). The high peat accumulation rate in semi-terrestrial fens explains its short 'turnover time' of 12 years, as determined by GIS interpretation of aerial photos (Bakker et al., 1994; Verhoeven & Bobbink, 2001). The rapid formation of carr woods can only be counteracted by mowing and hay removal.

An additional explanation may be the absence of keystone species like *Stratiotes aloides* and *Calla palustris,* initiating terrestrialisation by the formation of floating mats. This is caused by the high degree of fragmentation of fens in the Netherlands, which complicates the dispersal of diaspores of keystone or threatened species. The old-fashioned statement that 'everything is everywhere and nature selects' is rather oversimplified. Characteristic and threatened species are often absent in the diaspore bank of the restoration area, and the closest remnant populations are many kilometres away (T. van den Broek, pers. com.). The interconnection of scattered grazing areas, like pastures in fens, by flocks of sheep (Poschlod, 1995) has disappeared nowadays, although modern agricultural machines may inadvertently have taken over a small part of the cultural diaspore dispersal. Tackling this problem requires either new corridors connecting nearby populations (risking eutrophication for wet corridors) or active re-introduction of plants, seeds or spores. Experiments with the re-introduction of seeds and plants of the terrestrial species *Succissa pratensis* have shown positive results, provided the environmental conditions are restored first (P. Vergeer, pers. com.). If the donor population was small, however, germination levels proved to be lower, indicating possible inbreeding effects. In contrast, efforts to re-introduce aquatic macrophytes showed little or no success, often due to algal blooms (several managers of fen reserves, pers. com.). Therefore, re-introduction of diaspores should only be considered after the appropriate water quality has been restored. Fragmentation is also one of the main problems for fen-dwelling fauna. For this reason, corridors have been constructed between fen reserves and some species, like *Lutra lutra*, *Clossiana selene* and *Lycaena dispar*, have been or will be actively re-introduced.

Unlike aquatic fens, terrestrial and semi-terrestrial fens often cope with acidification. In projects where restoration of the ANC was implemented in eutrophic water, base saturation was restored but nutrient availability became too high simultaneously. The vegetation developed from acidophilic to minerotrophic but also to eutrophic – which, of course, was not the restoration goal. This is also often the case with the restoration of fens by renewed peat extraction. If initial conditions are eutrophic due to nutrient loading from the environs or high nutrient concentrations in the remaining sediment, restoration of mesotrophic floating fens is extremely difficult. It may be well worth to consider the conservation of carr woodlands rather than the employment of such radical restoration measures in these situations.

If surface water is used to compensate for the lowering of the groundwater table, problems may arise due to Fe depletion. As surface water is generally oxygenated, it contains only low concentrations of Fe. The high Fe input via anoxic groundwater in many fens plays a very important role in the binding of $PO_4^{3-}$, maintaining a low $PO_4^{3-}$ availability to the vegetation. The use of surface water as a substitute will therefore inevitably result in (internal) eutrophication, even if the $PO_4^{3-}$ concentrations in the water are low e.g. by P stripping methods. As the infiltration of surface water into fen soils appears to be very shallow (Koerselman et al., 1990b), large areas of fen peat can become influenced by the adverse water quality. In peatlands that have developed in the past under the influence of surface water, rather than groundwater, the situation is different. If the surface water is not eutrophicated and will not lead to internal eutrophication, or if the buffer zone is broad enough, mesotrophic fens may well develop and thrive after restoration.

Efforts to restore the base saturation in fens by applying lime have so far been not always successful (van Diggelen et al., 1996; Beltman et al., 2000). The major cause for this seems to be a strong acceleration in the rates of decomposition, and thereby mineralisation and eutrophication, of the peat (see Fig. 5). Liming has already for a long time been used for the purpose of raising the nutrient availability. In medieval times, monks applied lime to fish ponds to increase the production. Arable land and compost piles are limed for the same reason. Liming of fens may easily result in the development of a vegetation dominated by common, fast growing species such as *Juncus effusus* and *Glyceria maxima*.

A restoration measure that has unfortunately been employed in several fen types is the establishment of a high water table throughout the year. This artificial situation is generally far from the original state. Already within one year, the water in Alder carrs was completely covered by *Lemna* spp., while characteristic species like *Caltha palustris* and *Calla palustris* were drowned. $PO_4^{3-}$ concentrations increased several-fold because of prolonged anoxic conditions (A. Boxman & E. Lucassen, pers. com.). On these locations there was even a die-off of *Alnus glutinosa*. It is clear that this artificial hydrological regime, which may be termed 'over-rewetting', is very detrimental and undesirable. The same holds for fen meadows, which need aerobic conditions in the topsoil during summer, presumably also because the vegetation strongly prefers $NO_3^-$ to $NH_4^+$ as N source (de Graaf et al., 1998). The re-establishment of a more natural water table regime, with higher water tables during winter and lower during summer, is expected to provide better perspectives than the compensation of lower summer tables using riverine water.

In all restoration efforts, the diaspore bank or the dispersion of diaspores may form a significant constraint. After the re-establishment of optimal abiotic conditions, this can be an important pitfall for fen restoration, especially for isolated fen remnants (Bakker et al., 1996; van Diggelen et al., 1996). The only solution to this problem, if one does not want to wait for centuries, might be active re-introduction of diaspores (e.g. by applying hay from species rich fens) or plants. There is, however, not much experience with this measure in fens, especially on the long term.

## Conclusions

The Dutch fens and fen landscapes are unique in the world, in that they are a combination of man-made and natural succession. As these fens represent a great variety in plant communities, encompassing a rich biodiversity of higher plants, bryophytes and fauna, they deserve a high priority in nature management and restoration planning. For a number of fen types in the Netherlands, this holds true for both national and global scales, which is borne out by their designation on the Ramsar list of Wetlands of International Importance. The goals for restoration lie in the recovery of characteristic, often semi-natural fen systems (flora and fauna), by the restoration of the optimal hydrology, hydrochemistry and sediment characteristics on locations that still possess the diaspore sources. Note that optimal hydrology does not mean 'as wet as possible'; it refers to the water table regime that is needed by the plant communities involved. In all cases, restoration of both the original hydrology and the original hydrochemistry is strongly preferred, although this is often not feasible. This means that the hydrology not only has to restore telluric conditions (adequate ANC) but also mesotrophic conditions, and (if possible) the discharge of groundwater rich in Fe and Ca. Recent pollution sources that have led to eutrophication have to be minimised or, even better, eliminated. In some fens biomanipulation turned out to be very effective tool in re-establishing underwater light conditions favourable for submerged macrophytes. In most fen waters, however, the best way of fighting eutrophication seems to lie in a combination of biomanipulation (topdown control) and active reduction of the influx and internal mobilisation of $PO_4^{3-}$ (bottom-up). For both approaches, and certainly for their combination, additional research is needed. A recent strategy to minimise the use of allochthonous water (leading to eutrophication) seems to lie in the application of a more natural water table management strategy, allowing higher tables in winter and lower in summer. In addition, this is expected to decrease phosphate concentrations and stimulate germination of aquatic macrophytes. However, this measure needs further research.

A severe problem affecting Dutch fens is the absence of terrestrialisation of aquatic fens. Due to this, the new formation of floating fens including their typical and threatened plant communities is extremely rare. New research on fen management and restoration should, therefore, include studies on the mechanisms of peat formation and succession.

Problems are often caused by the fact that the only water available for restoration is not of sufficient quality. It must be stressed that the risk of both direct eutrophication (nutrient influx) and indirect eutrophication (internal eutrophication) should be considered when making restoration plans. Nutrient pollution, high alkalinity or increased sulphate concentrations counteract the beneficial effects of mineral enrichment in acidified fens. In that case, the plant communities aimed at may not be feasible, and the restorers have to be satisfied with a more humble goal (Wheeler & Shaw, 1995). On other locations, more species-rich communities may develop further from the eutrophicating source (e.g. a stream or river), the adjacent high-productive zones acting as a nutrient filter.

The successful restoration of abiotic conditions required does not automatically imply the successful restoration of a fen. If one wants to restore populations of rare and endangered plant species on isolated locations without a viable diaspore bank, the re-introduction of seeds or plants is unavoidable. This calls for more research on the dispersal and establishment of fen plants. For fen-dwelling fauna, habitat fragmentation seems to be an even more important cause for lack of restoration success.

The management of semi-natural fen landscapes is costly, especially if earlier succession state communities are involved. Mowing and peat extraction activities are no longer of economical importance (apart from the harvesting of *Phragmites*, and to a minor extent of *Sphagnum*), and these tasks have been taken over by nature management agencies. If the budgets are low, less costly management of more eutrophic fen types inhabited by many waterfowl species provides the most obvious alternative.

The restoration of fens has been successfully achieved by several projects in the Netherlands. In such cases the desired plant communities are developing well. For many projects, time still has to tell whether restoration efforts will produce the desired effect. Other projects are much less successful, mostly because of eutrophication problems. Research should focus on the differences between projects in order to find out which of the correlating factors might be causal for the (lack of) success. All types of projects are, however, extremely valuable for the evaluation of restoration measures and differences in starting conditions. Rather than sticking to the trial-and-error approach, we plead for thorough research into the factors and mechanisms controlling the development of fen vegetation. This requires a combination of well documented restoration efforts, in which both the starting conditions and developments are described, field research on different locations to find biogeochemical, hydrological and ecological correlations, and experimental research. By performing experimental research, e.g. by using enclosures (Fig. 6) or greenhouse experiments, causal relationships can be found that reveal key factors and mechanisms in ecosystem functioning. Only in this way can favourable locations for restoration be distinguished from less favourable. Moreover, the understanding of these processes allows for the use of optimal restoration methods, and for a better future assessment of fen restoration projects. The great variety of fen types, and the unique character of the semi-natural systems and their biodiversity, justify optimal restoration and management efforts.

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## References

J. D., K. J. Nadelhoffer, P. Steudler & J. M. Melillo, 1989. Nitrogen saturation in northern forest systems. Bioscience 39: 378–386.

Aerts, R., J. A. Verhoeven & D. F. Whigham, 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. Ecology 80: 2170–2181.

Akkermans, A. D. L., 1971. Nitrogen fixation and nodulation of *Alnus* and *Hippophaë* under natural conditions. Ph.D. thesis, University of Leiden, Leiden: 85 pp.

Arnolds, E. J. M., Th. W. Kuyper & M. E. Noordeloos (eds), 1995. Overzicht van de paddestoelen in Nederland. Nederlandse Mycologische Vereniging, Wijster: 871 pp.

Bakker, J. P., P. Poschlod, R. J. Strykstra, R. M. Bekker & K. Thompson, 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta bot. neerl. 45: 461–490.

Bakker, S. A., N. J. van den Berg & B. P. Speleers, 1994. Vegetation transitions of floating wetlands in a complex of turbaries between 1937 and 1989 as determined from aerial photographs with GIS. Vegetatio, 114: 161–167.

Bakker, S. A., C. Jasperse & J. T. A. Verhoeven, 1997. Accumulation rates of organic matter associated with different successional stages from open water to carr forest in former turbaries. Plant Ecol. 129: 113–120.

Beltman, B., T. van den Broek & S. Bloemen, 1995. Restoration of acidified rich-fen ecosystems in the Vechtplassen area: successes and failures. In Wheeler, B. D., S. C. Shaw, W. J. Fojt & R. A. Robertson (eds), Restoration of Temperate Wetlands. John Wiley & Sons Ltd, Chichester: 273–286.

Beltman, B., T. van den Broek, S. Bloemen & C. Witsel, 1996a. Effects of restoration measures on nutrient availability in a formerly nutrient-poor floating fen after acidification and eutrophication. Biol. Conserv. 78: 271–277.

Beltman, B., T. van den Broek, K. van Maanen & K. Vaneveld, 1996b. Measures to develop a rich-fen wetland landscape with a full range of successional stages. Ecol. Eng. 7: 299–313.

Beltman, B., T. G. Rouwenhorst, M. B. van Kerkhoven, T. van der Krift & J. T. A. Verhoeven, 2000. Internal eutrophication in peat soils through competition between chloride and sulphate with phosphate for binding sites. Biogeochemistry 50: 183–194.

Berendse, F., M. J. M. Oomes, H. J. Altena & W. de Visser, 1994. A comparative study of nitrogen flows in two similar meadows affected by different groundwater levels. J. appl. Ecol. 31: 40–48.

Bink, F. A., 1992. Oecologische atlas van de dagvlinders van Noordwest Europa. Schuyt, Haarlem: 512 pp.

Bobbink, R., M. Hornung & J. G. M. Roelofs, 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural vegetation – A review. J. Ecol. 86: 717–738.

Boers, P. C. M., 1991. The release of dissolved phosphorus from lake sediments. Ph.D. thesis, Wageningen Agricultural University, Wageningen: 139 pp.

Boeye, D., D. van Straaten & R. F. Verheyen, 1995. A recent transformation from poor to rich fen caused by artificial groundwater recharge. J. Hydrol. 169: 111–129.

Bootsma, M. C., 2000. Stress and recovery in wetland ecosystems. Ph.D. thesis, University of Utrecht, Utrecht: 193 pp.

Boström, B., M. Jansson & C. Forsberg, 1982. Phosphorus release from lake sediments. Arch. Hydrobiol. Beih. Ergebn. Limnol. 18: 5–59.

Brock, T. C. M., J. J. Boon & B. G. P. Paffen, 1985. The effects of the season and of water chemistry on the decomposition of *Nymphaea alba* L.; weight loss and pyrolysis mass spectrometry of the particulate matter. Aquat. Bot. 22: 197–229.

Brouwer, E., J. Soontiëns, R. Bobbink & J. G. M. Roelofs, 1999. Sulphate and bicarbonate as key factors in sediment degradation and restoration of Lake Banen. Aquat. Cons. mar. freshw. Ecosys. 9: 121–132.

Caraco, N. F., J. J. Cole & G. E. Likens, 1989. Evidence for sulphate-controlled phosphorus release from sediments of aquatic systems. Nature 341: 156–158.

Coops, H. & G. van der Velde, 1995. Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. Freshwat. Biol. 34: 13–20.

De Graaf, M. C. C., P. J. M. Verbeek, M. J. R. Cals & J. G. M. Roelofs, 1994. Effectgerichte maatregelen tegen verzuring en eutrofiëring van matig mineraalrijke heide en schraallanden. Eindrapport monitoringsperiode eerste fase. Department of Ecology, University of Nijmegen, Nijmegen: 248 pp.

De Graaf, M. C. C., R. Bobbink, P. J. M. Verbeek & J. G. M. Roelofs, 1997. Aluminium toxicity and tolerance in three heathland species. Wat. Air Soil Pollut. 98: 229–239.

De Graaf, M. C. C., R. Bobbink, J. G. M. Roelofs & P. J. M. Verbeek, 1998. Differential effects of ammonium and nitrate on three heathland species. Plant Ecol. 135: 185–196.

Den Held, A. J., M. Schmitz & G. van Wirdum, 1992. Types of terrestrializing fen vegetation in the Netherlands. In Verhoeven, J. T. A. (ed.), Fens and Bogs in the Netherlands: Vegetation, History, Nutrient Dynamics and Conservation. Kluwer Academic Publishers, Dordrecht: 237–321.

De Lyon, M. J. H. & J. G. M. Roelofs, 1986. Waterplanten in relatie tot waterkwaliteit en bodemgesteldheid. Deel 1 & 2. Laboratorium voor Aquatische Oecologie, Katholieke Universiteit Nijmegen, Nijmegen: 106 + 126 pp.

De Mars, H., A. C. Garritsen & C. van Elswijk, 1996. Van veenrivier tot boezemwater; de Greft en het behoud van de Kamerikse Nessen. Landschap 13: 207–221 (Abstract in English).

Frazier, S., 1999. Ramsar sites overview. Wetlands International + 1999 Edition of the directory of wetlands of international importance: 42 pp.

Gliwicz, Z. M., 1990. Why do cladocerans fail to control algal blooms? Hydrobiologia 200/201: 83–97.

Gore, A. J. P. (ed.), 1983. Mires – Swamp, Bog, Fen and Moor. Ecosystems of the World, 4A. Elsevier, Amsterdam: 440 pp.

Grootjans, A. P., J. P. Bakker, A. J. M. Jansen & R. H. Kemmers, 2002. Restoration of brook valleys in the Netherlands. Hydrobiologia 478/Dev. Hydrobiol. 166: 149–170.

Grootjans, A. P. & R. van Diggelen, 1995. Assessing the restoration prospects of degraded fens. In Wheeler, B. D., S. C. Shaw, W. J. Fojt & R. A. Robertson (eds), Restoration of Temperate Wetlands. John Wiley & Sons Ltd, Chichester: 73–90.

Grootjans, A. P., P. C. Schipper & H. J. van der Windt, 1986. Influence of drainage on N-mineralisation and vegetation response in wet meadows II. Cirsio-Molinietum stands. Acta oecol. Oecol. plant. 7(21): 3–14.

Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer & E. van Donk, 1990. Biomanipulation Tool for Water Management. Developments in Hydrobiology 61. Kluwer Academic Publishers, Dordrecht: 628 pp. Reprinted from Hydrobiologia 200/201.

Gulati, R. D. & E. van Donk, 2002. Lakes in the Netherlands, their origin, eutrophication and restoration: state-of-the art review. Hydrobiologia 478/Dev. Hydrobiol. 166: 73–106.

Higler, L. W. G., 1977. Macrofauna-cenoses on *Stratiotes* plants in Dutch broads. Ph.D. thesis, Research Institute for Nature Management, Leersum: 86 pp.

Hosper, S. H., 1997. Clearing lakes – An ecosystem approach to the restoration and management of shallow lakes in the Netherlands. Ph.D. thesis Wageningen Agricultural University, Wageningen: 168 pp.

Houdijk, A. L. F. M. & J. G. M. Roelofs, 1991. Deposition of acidifying and eutrophicating substances in Dutch forests. Act. bot. neerl. 40: 245–255.

Jansen, A. J. M. & J. G. M. Roelofs, 1996. Restoration of Cirsio-Molinietum wet meadows by sod cutting. Ecol. Eng. 7: 279–298.

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

Jefferies, D. J., 1988, The changing otter population of Britain 1700–1989. Biol. J. linn. Soc. 38: 61–69.

Jeppesen, E., J. P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjaer & O. K. Olrik, 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. Hydrobiologia 200/201: 219–227.

Kemmers, R. H., 1996. Humusprofielen en bodemprocessen: beoordeling van mogelijkheden voor wateraanvoer. Landschap 13/3: 157–168 (Abstract in English).

Klinge, M., M. P. Grimm & S. H. Hosper, 1995. Eutrophication and ecological rehabilitation of Dutch lakes: presentation of a new conceptual framework. Wat. Sci. Technol. 31: 207–218.

Koch, M. S., I. A. Mendelssohn & K. L. McKee, 1990. Mechanism for the sulfide-induced growth limitation in wetland macrophytes. Limnol. Oceanogr. 35: 399–408.

Koerselman, W & J. T. A. Verhoeven, 1992. Nutrient dynamics in mires of various trophic status: nutrient inputs and outputs and the internal nutrient cycle. In Verhoeven, J. T. A. (ed.), Fens and Bogs in the Netherlands: Vegetation, History, Nutrient Dynamics and Conservation. Kluwer Academic Publishers, Dordrecht: 397–432.

Koerselman, W. & J. T. A. Verhoeven, 1995. Eutrophication of fen ecosystems: external and internal nutrient sources and restoration strategies. In Wheeler, B. D., S. C. Shaw, W. J. Fojt & R. A. Robertson (eds), Restoration of Temperate Wetlands. John Wiley & Sons Ltd, Chichester: 91–112.

Koerselman, W., H. de Caluwe & W. M. Kieskamp, 1989. Denitrification and dinitrogen fixation in two quaking fens in the Vechtplassen area, the Netherlands. Biogeochemistry 8: 153–165.

Koerselman, W., S. A. Bakker & M. Blom, 1990a. Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. J. Ecol. 78: 428–442.

Koerselman, W., D. Claessens, P. ten Den & E. van Winden, 1990b. Dynamic hydrochemical and vegetation gradients in fens. Wetl. Ecol. Managem. 1: 73–84.

Kok, C. J. & B. J. van de Laar, 1991. Influence of pH and buffering capacity on the decomposition of *Nymphaea alba* L. detritus in laboratory experiments: a possible explanation for the inhibition of decomposition at low alkalinity. Verh. int. Ver. theor. angew. Limnol. 24: 2689–2692.

Kooijman, A. M. & C. Bakker, 1995. Species replacement in the bryophyte layer in mires: the role of water type, nutrient supply and interspecific interactions. J. Ecol. 83: 1–8.

Koops, J. G., O. Oenema & M. L. van Beusichem, 1996. Denitrification in the top and sub soil of grassland on peat soils. Plant Soil 184: 1–10.

Kruuk, H., 1995. Wild Otters – Predation and Populations. Oxford University Press, Oxford: 300 pp.

Lamers, L. P. M., A. J. P. Smolders, E. Brouwer & J. G. M. Roelofs, 1996. Sulfaatverrijkt water als inlaatwater? – De rol van waterkwaliteit bij maatregelen tegen verdroging. Landschap 13, 169–180 (Abstract in English).

Lamers, L. P. M., S. M. E. van Roozendaal & J. G. M. Roelofs, 1998. Acidification of freshwater wetlands: combined effects of non- airborne sulfur pollution and desiccation. Water Air Soil Pollut. 105: 95–106.

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

Lamers, L. P. M., A. J. P. Smolders & J. G. M. Roelofs, 1999a. Hoe gevoelig is natte natuur voor grondwaterverontreiniging? – Op zoek naar sturende processen en factoren. Landschap 16/3: 15–25 (Abstract in English).

Lamers, L. P. M., C. Farhoush, J.M. van Groenendael & J. G. M. Roelofs, 1999b. Calcareous groundwater raises bogs; the concept of ombrotrophy revisited. J. Ecol. 87: 639–648.

Lamers, L. P. M., 2001. Tackling some biogeochemical questions in peatlands. Ph.D. thesis, University of Nijmegen, Nijmegen.

Laurén-Määttä, C., J. Hietala & M. Walls, 1997. Responses of *Daphnia pulex* populations to toxic cyanobacteria. Freshwat. Biol. 37: 635–647.

Lucassen, E. C. H. E. T., A. J. P. Smolders & J. G. M. Roelofs, 2000. Increased groundwater levels cause iron toxicity in Glyceria fluitans (L.). Aquat. Bot. 66: 321–328.

McKinley, V. L. & J. R. Vestal, 1982. Effects of acid on plant litter decomposition in an arctic lake. Appl. environ. Microbiol. 43: 1188–1195.

Meijer, M.-L., I. De Boois, M. Scheffer, R. Portielje & H. Hosper, 1999. Biomanipulation in shallow lakes in The Netherlands: an evaluation of 18 case studies. Hydrobiologia 408/409: 13–30.

Meijer, M.-L., 2000. Biomanipulation in the Netherlands – 15 years of experience. Ph.D. thesis, Wageningen Agricultural University, Wageningen: 208 pp.

Moss, B., 1998. Ecology of Fresh Waters – Man and Medium (3rd edn). Blackwell Scientific, Oxford: 557 pp.

Oomes, M. J. M., P. J. Kuikman & F. H. H. Jacobs, 1997. Nitrogen availability and uptake by grassland in mesocosms at two water levels and two water qualities.Plant Soil 192: 249–259.

Pegtel, D., 1983. Ecological aspects of a nutrient-deficient wet grassland (Cirsio-Molinietum). Verh. ges. Ökologie X: 217–228.

Pons, L. J., 1992. Holocene peat formation in the lower parts of the Netherlands. In Verhoeven, J. T. A. (ed.), Fens and Bogs in the Netherlands: Vegetation, History, Nutrient Dynamics and Conservation. Kluwer Academic Publishers, Dordrecht: 7–79.

Poschlod, P., 1995. Diaspore rain and diaspore bank in raised bogs and implications for the restoration of peat-mined sites. In Wheeler, B. D., S. C. Shaw, W. J. Fojt & R. A. Robertson (eds), Restoration of Temperate Wetlands. John Wiley & Sons Ltd, Chichester: 471–494.

Roelofs, J. G. M., 1991. Inlet of alkaline river water into peaty lowlands: effects on water quality and *Stratiotes aloides* L. stands. Aquat. Bot. 39: 267–293.

Roelofs, J. G. M., E. Brouwer & R. Bobbink, 2002. Restoration of aquatic macrophyte vegetation in acidified and eutrophicated shallow softwater wetlands in the Netherlands. Hydrobiologia 478/Dev. Hydrobiol. 166: 171–180.

Schaminée, J. H. J., E. J. Weeda & V. Westhoff, 1995. De vegetatie van Nederland. Deel 2. Plantengemeenschappen van wateren, moerassen en natte heiden. Opulus Press, Uppsala, Leiden: 360 pp.

Schaminée, J. H. J., A. H. F. Stortelder & E. J. Weeda, 1996. De vegetatie van Nederland. Deel 3. Plantengemeenschappen van graslanden, zomen en droge heiden. Opulus Press, Uppsala, Leiden: 356 pp.

Schaminée, J. H. J., E. J. Weeda & V. Westhoff, 1998. De vegetatie van Nederland. Deel 4. Plantengemeenschappen van de kust en van binnenlandse pioniermilieus. Opulus Press, Uppsala, Leiden: 346 pp.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. TREE 8: 275–278.

Schouwenaars J. M., H. Esselink, L. P. M. Lamers & P. C. van der Molen, 1997. Hoogveenherstel in Nederland, bestaande kennis en benodigd onderzoek. University of Groningen, University of Nijmegen, Stichting Bargerveen, Bureau GroenHolland: 122 pp.

Shapiro, J., V. Lamarra & M. Lynch, 1975. Biomanipulation: an ecosystem approach to lake restoration. In Brezonik P. L. & J. L. Fox (eds), Water Quality Management Through Biological Control. University of Florida, Gainesville: 85–96.

Smolders, A. J. P., 1995. Mechanisms involved in the decline of aquatic macrophytes; in particular of *Stratiotes aloides* L. Ph.D. thesis University of Nijmegen, Nijmegen: 159 pp.

Smolders, A. J. P. & J. G. M. Roelofs, 1993. Sulphate mediated iron limitation and eutrophication in aquatic systems. Aquat. Bot. 46: 247–253.

Smolders, A. J. P. & J. G. M. Roelofs, 1995. Internal eutrophication, iron limitation and sulphide accumulation due to the inlet of river Rhine water in peaty shallow waters in the Netherlands. Arch. Hydrobiol. 133: 349–365.

Smolders, A. J. P. & J. G. M. Roelofs, 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 Phytol. 133: 253–260.

Smolders, A. J. P., R.C. Nijboer & J. G. M. Roelofs, 1995. Prevention of sulphide accumulation and phosphate mobilization by the addition of iron(II) chloride to a reduced sediment: an enclosure experiment. Freshwat. Biol. 34: 559–568.

Stortelder, A. H. F., J. H. J. Schaminée & P. W. F. M. Hommel, 1999. De vegetatie van Nederland. Deel 5. Plantengemeenschappen van ruigten, struwelen en bossen. Opulus Press, Uppsala, Leiden: 376 pp.

Stumm, W. & J. J. Morgan, 1981. Aquatic Chemistry, an Introduction Emphasizing Chemical Equilibria in Natural Waters. 2nd edn. John Wiley & Sons, New York: 780 pp.

Van den Broek, T. & B. Beltman, 1995, Mesotrofe verlandingsvegetaties, nieuwe kansen in het Noorderpark. Landschap 12(5): 29–38 (Abstract in English).

Van der Putten, W. H., 1997. Die-back of Phragmites australis in European wetlands: an overview of the European Research Programme on Reed Die-back and Progression. Aquat. Bot. 59: 263–275.

Van de Ven, G. P. (ed.) 1994. Man-Made Lowlands – History of Water Management and Land Reclamation in the Netherlands. Matrijs, Utrecht: 293 pp.

Van Diggelen, R., W. J. Molenaar & A. M. Kooijman, 1996. Vegetation succession in a floating mire in relation to management and hydrology. J. Veg. Sci. 7: 809–820.

Van Donk, E. & W. J. van de Bund, 2002. Impact of submerged macrophytes including charophytes on phyto- and zooplankton communities: allelopathy *versus* other mechanisms. Aquat. Bot. 72: 261–274.

Van Duren, I. C., D. Boeye & A. P. Grootjans, 1997. Nutrient limitations in an extant and drained poor fen: implications for restoration. Plant Ecol. 133: 91–100.

Van Turnhout, C. & W. Hagemeijer, 2001. Long-term population developments in typical marshland bird species in the Netherlands. Ardea, in press.

Van ‘t Veer, R., B. van Geel, J. P. Pals & D. van Smeerdijk, 2000. Fossiele plantengemeenschappen als referentiekader voor moderne moerasontwikkeling. In Schaminée, J. & R. van ’t Veer (eds), 100 Jaar op de knieën – De geschiedenis van de plantensociologie in Nederland. Opulus Press, Noordwolde: 174–189.

Van Wirdum, G.,1991. Vegetation and hydrology of floating richfens. Ph.D. thesis, University of Amsterdam, Amsterdam: 310 pp.

Van Wirdum, G., A. J. den Held & M. Schmitz, 1992. Terrestrializing fen vegetation in former turbaries in the Netherlands. In Verhoeven, J. T. A. (ed.), Fens and Bogs in the Netherlands: Vegetation, History, Nutrient Dynamics and Conservation. Kluwer Academic Publishers, Dordrecht: 323–360.

Verhoeven, J. T. A. & W. M. Liefveld, 1997. The ecological significance of organochemical compounds in Sphagnum. Acta Bot. Neerl. 46: 117–130.

Verhoeven, J. T. A. & R. Bobbink, 2001, Plant diversity of fen landscapes in The Netherlands. The role of water chemistry, succession and management. Aquat. Bot., in press.

Verhoeven, J. T. A., A. M. Kooijman & G. van Wirdum, 1988. Mineralization of N and P along a trophic gradient in a freshwater mire. Biogeochemistry 6: 31–43.

Verhoeven, J. T. A., W. Koerselman & A. F. M. Meuleman, 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: relations with atmospheric inputs and management regimes. TREE 11: 494–497.

Vermeer, J. G., 1986. The effect of nutrient addition and lowering of the water table on shoot biomass and species composition of a wet grassland community (Cirsio-Molinietum Siss. et de Vries, 1942). Acta oecol. 7: 145–155.

Vermeer, J. G. & J. H. J. Joosten, 1992. Conservation and management of bog and fen reserves in the Netherlands. In Verhoeven, J. T. A. (ed.), Fens and Bogs in the Netherlands: Vegetation, History, Nutrient Dynamics and Conservation. Kluwer Academic Publishers, Dordrecht: 433–478.

Wassen, M. J. & A. Barendregt, 1992. Topographic position and water chemistry of fens in a Dutch river plain. J. Veg. Sci. 3: 447–456.

Wassen, M. J., H. G. M. Olde Venterink & E. O. A. M. de Swart, 1996. Nutrient concentrations in mire vegetation as a measure of nutrient limitations in mire ecosystems. J. Veg. Sci. 6: 5–16.

Waughman, 1980. Chemical aspects of the ecology of some south German peatlands. J. Ecol. 68: 1025–1046.

Westhoff, V., P. A. Bakker, C. G. van Leeuwen & E. E. van der Voo, 1970. Wilde planten: flora en vegetatie in onze natuurgebieden. Deel 1: Algemene inleiding, duinen, zilte gronden. Natuurmonumenten, 's-Gravenland: 320 pp.

Wheeler, B. D. & S. C. Shaw, 1995. Restoration of damaged peatlands, with particular reference to lowland raised bogs affected by peat extraction. HMSO, London: 211 pp.

Wheeler, B. D. & M. C. F. Proctor, 2000. Ecological gradients, subdivisions and terminology of north-west European mires. J. Ecol. 88: 187–203.

Wiegers, J., 1992. Carr vegetation: plant communities and succession of the dominant tree species. In Verhoeven, J. T. A. (ed.), Fens and Bogs in the Netherlands: Vegetation, History, Nutrient Dynamics and Conservation. Kluwer Academic Publishers, Dordrecht: 361–396.